GROWTH AND FOLIAR NUTRIENT CONCENTRATIONS OF *Eucalyptus grandis* IN RELATION TO SPODOSOL PROPERTIES IN SOUTH FLORIDA

BY

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To my wife
MAURA

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The relationships among tree growth, foliar elemental concentrations, and soil properties were examined in a 4-year-old *Eucalyptus grandis* plantation growing on a Haplaquod in southern Florida to identify soil properties affecting tree growth. Site preparation included bedding with 1.0 ton of ground rock phosphate (GRP) per ha applied to 3/4 of the area and 2.0 ton/ha applied to the other 1/4 of the area. Tree measurements and soil and leaf samples were taken from fifty 120 m^2 plots distributed over three soil series, i.e., Immokalee (32 plots), Myakka (7 plots), and Smyrna (11 plots). Dominant and mean tree heights and volume per hectare were used as dependent variables in the simple and multiple regression studies.

The mean annual increments in height (2.6 m) and in volume (8 m^3/ha) were lower than those obtained for this species in other parts of the world. These low increments presumably reflected the unfavorable physical and chemical conditions of the soils for

E. grandis growth. Tree shoot and root growth were smaller on the Smyrna soil than in the Immokalee and Myakka soils partially because of the smaller volume of soil for root exploitation and possible tree water stress during long dry periods. In the Immokalee soil, the application of 2.0 ton GRP/ha resulted in height and volume increments 19% and 47% higher than those recorded on plots where 1.0 ton/ha rate was used.

The relative importance of a given soil property for tree growth varied from one soil type to another but, in general, soil pH, organic matter content, surface soil K, and the P and Mg concentrations, CEC, and water-holding capacity of the spodic horizon were significantly correlated with growth. Soil pH was found to be negatively correlated with tree growth through its interrelationship with other soil factors, such as organic matter and P, and its effect on GRP dissolution. The correlations between tree growth and surface soil K and Mg concentrations were positive for the Myakka and Smyrna soils but negative for the Immokalee soil. Soil and foliar analyses indicated N and K deficiencies; therefore, eucalypt growth responses may be expected from applications of N and K fertilizers. The levels of P appeared to be adequate for tree growth whereas those of Ca and Mg were marginal. The best growth predicting equations from soil properties accounted for about 60% in height growth and 55% in volume growth variations. Higher R^2 values were obtained by stratifying the data by soil series or GRP.

Poor tree growth on Smyrna soil is most likely explained by the fact that 75 to 85% of roots of *Eucalyptus grandis* are generally confined to the surface soil horizon, apparently due to a better

nutrient and oxygen status of this layer than in the A2 horizon. Furthermore, the taproots failed to effectively penetrate in the spodic horizon presumably due to the poor aeration, high bulk density (about 1.70 g/cm^3), and high exchangeable Al concentrations, which approached a toxic level of about 300 ppm. In the Smyrna (shallow spodic) soil, these factors, associated with the limited volume of exploitable soil, caused a 30% reduction in root biomass as compared with those in the Immokalee (23 ton/ha) and Myakka (25 ton/ha). It seems likely that a severe water stress may develop in trees on the Smyrna soil during long dry periods when the water table is below the spodic horizon.

INTRODUCTION

Tree growth and forest productivity are results of physiological responses to the interaction of biotic, chemical, and physical factors of the environment. Climate, physiography, and soil characteristics are usually the most important factors of the environment affecting site quality—the capacity of the land to produce the desirable forest products.

Site quality estimation is essential in the yield-prediction system for estimating growth and yield and making decisions in terms of land acquisition, industrial investments, and silvicultural inputs.

A relatively large percentage of Florida's forests are intensively managed. Besides site preparation and fertilization practices in pine forests, some fast growing exotic species, mostly of the *Eucalyptus* and *Melaleuca* genera, have been tested. The area planted to eucalypts in southern Florida has sharply increased in recent years, and 3,700 ha* had been planted prior to 1979. These plantations consist mostly of *Eucalyptus grandis*, with the main purpose being industrial production of pulp and paper.

Large variations in height growth of *E. grandis* trees have been observed between and within stands of the same age in this area. In the best stands, trees reach an annual rate of height growth of 3.0 m (Geary, 1977) which is considered normal for this species (Anonymous,

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* Geary, T. F., personal communication.

1976), but poor growth is observed in other stands where the growth rate is about 1.5 m per year (Meskimen and Franklin, 1978). Since seed stocks of superior genetic quality and similar management practices have been used in the most recently planted stands, variation in tree growth is probably a response to variations in soil properties.

The eucalypt stands have been planted on the coastal flatwood soils (Spodosols), which are very acid and low in nutrient reserves. Many of the properties of these soils are greatly affected by the characteristics of the "spodic horizon," a cemented organic hardpan. Therefore, besides the effect of low fertility of the surface horizons, variation in tree growth in the area might also be explained by restrictions, directly or indirectly, imposed by the spodic horizon to root growth. Extreme hardness and a high level of exchangeable Al of the spodic horizon may directly limit the volume of soil (effective depth) exploitable by the roots.

The indirect effects of the spodic horizon on root and tree growth occur principally by controlling the height of the water table during very wet or very dry seasons, i.e., the depth and thickness of the spodic horizon and the associated hydraulic conductivity may play a major role in controlling the water table. If the combination of these characteristics permits water to flow downward, better aeration conditions will be present for root growth. Otherwise, during wet periods, anoxia will occur as the level of the water table increases resulting in the subsequent death of part of the root system if this condition lasts for a considerable time. During dry periods,

water deficiency may occur, particularly for the upper portions of the root system, if the level of the water table is too low.

This study was conducted in an attempt to identify important soil and site factors responsible for variations in growth of *E. grandis* in South Florida. It involved investigations of a number of soil-site relationships with particular emphasis on relating tree growth to (a) soil physical and chemical properties, (b) Al concentrations in the spodic horizon, (c) depth of rooting, and (d) foliar nutrient concentrations.

LITERATURE REVIEW

General Information on the Genus Eucalyptus

Classification of Eucalyptus

The genus *Eucalyptus* belongs to the family Myrtaceae and was described and named by L'Heritier in 1788. The genus is characterized by an operculum, or cap, which covers the bud until the flower expands. The leaves are usually alternate in the adult form but are opposite, at least for a few pairs, on seedlings or juvenile shoots (Hall et al., 1970). Botanically, each eucalypt is distinguished by general growth habits and dimensions; its bark in the adult stage, juvenile and mature leaves, young branches, inflorescences, buds, stamen, fruits, and seeds.

In the most recent and accepted taxonomic classification (Pryor and Johnson, 1971), the genus *Eucalyptus* was divided into seven subgenera that can be defined by the association of many characteristics that are believed to be completely reproductively isolated. The subgenera are divided into sections, series, subseries, superspecies, species, and subspecies. About 500 species and subspecies of eucalypts are known.

Eucalyptus grandis Hill ex Maiden belongs to the subgenus *Symphyomyrtus*, which comprises many sections that can be separated on the basis of a combination of several characters. An illustration of the subdivisions of the subgenus *Symphyomyrtus* was presented by Hillis and Brown (1978) as follows:

Subgenus *Symphyomyrtus*	Section
cotyledons bisected	Bisectaria
cotyledons reniform or bilobed	
anthers adnate	Adnaria
anthers versatile	
leaves with transverse venation	Transversaria
leaves with acute venation	
pith granular	Dumaria
pith non-granular	
juvenile leaves distinctly petiolate, few opposite	Exsertaria
juvenile leaves more or less sessile, many opposite	Maidenaria

Eucalyptus grandis is classified in the section Transversaria, series Salignae, subseries Salignae (Pryor and Johnson, 1971). Its general botanical characteristics (Hall et al., 1970) are the following: light grey bark, fibrous stocking for several meters and smooth above; juvenile leaves opposite for 3 or 4 pairs then alternate, shortly stalked, oblong-lancealate, slightly wavy. The leaves have transverse venation and a distinct intramarginal vein; inflorescences are umbels on flattened peduncles, buds pear-shaped with bluntly pointed opercula; fruit pear-shaped, slightly contracted on short or very short pedicels, and with narrow and depressed disc and thin valves.

Natural Occurrence of Eucalypts

Most eucalypt species are native to the Australian continent and adjacent islands. Nevertheless, some species occur naturally in New

Guinea, in some of the Indonesian Archipelago, and in the Philippines. The latitudinal range extends from 7°N to 43° 39'S. In this range, a large variation in ecological conditions occurs. Some species flourish in sandy and desert regions where the annual rainfall is 300 mm or less, whereas others prefer regions where the rainfall is 3,000 mm per annum or more. The eucalypt preference for soil ranges from the poorest sands to the richest loams (Penfold and Willis, 1961). Most eucalypts, however, will not thrive on soils that are alkaline and have large quantities of free calcium carbonate or have sulfate in the profile (Anonymous, 1976). Because the wide natural distribution of eucalypts covers a great variety of ecological conditions, it has been possible to select species to be planted almost anywhere in the world.

The geographic distribution of *E. grandis* is between 16 and 33° S with the major concentration in the range of 26 to 32° S (Anonymous, 1976). The natural populations are concentrated in the altitudinal range of 0 to 300 m, although some can be found at altitudes of 900 m. The mean annual rainfall varies from 1,000 to 1,800 mm with a summer-autumn maximum. The mean minimum temperature of the coldest month is about 5° C. Coastal areas are frost free but occasional frosts occur at higher altitudes and in depressions away from the coast (Turnbull and Pryor, 1978).

Eucalyptus grandis normally occurs in soils that are deep, well drained, and of alluvial or volcanic origin. The species is intolerant of swampy conditions but will withstand short periods of flooding (Turnbull and Pryor, 1978).

Eucalypts as Exotic Species

The rapid dispersion and the increasing area of eucalypt plantations throughout the world are consequences of the good adaptation to new conditions and inherent fast growth characteristics that most species possess.

Eucalypt species have been planted in 58 countries covering more than 3.6 million hectares of commercial plantations (Anonymous, 1976). However, more than 60% of these plantations are concentrated in five countries, i.e., Brazil (29%), Spain (11%), South Africa (9.5%), Portugal (6.8%), and India (5%). According to a FAO report (Anonymous, 1976), there were about 140,000 ha of eucalypts in the United States in 1973 representing 3.8% of the total area of plantations in the world.

The annual increment of the 3.6 million hectares of eucalypt plantations is estimated to be around 40 million cubic meters which gives an approximate average yield of 11 m^3/ha/year.

Eucalyptus grandis is one of the most important exotic eucalypts, both for the extent to which it has been planted and for its growth performance. More than a half million hectares (Anonymous, 1976) had been planted with *E. grandis* prior to 1976 and, together with *E. saligna*, is the most widely planted eucalypts in the world. When planted under very favorable conditions, *E. grandis* may grow 10 m or more in height per year. However, its normal rate of growth varies from 2-3 m when planted on suitable sites. Annual increments of 14 to 25 m^3 have been obtained on good savanna sites in Uganda and 50 m^3 on red soils in Argentina (Anonymous, 1976). In Brazil, selected

seed sources of *E. grandis* have given very high growth rates of up to 73 m^3/ha/year (Rance, 1976).

Eucalypt species are attractive for planting not only for their rapid growth but, also, because their coppicing habit. Coppicing allows several crops to be harvested from an initially planted seedling. The number of coppicing rotations obtained from one planting varies from 2 to 10 or more, according to species and site. Usually coppicing rotations produce more than the first seedling harvest and they can yield as much as 1.5 times more than the initial rotation. In Kenya, the mean annual increment of *E. grandis* was 21 m^3 and 32 m^3/ha/year, respectively, for the seedling and coppice rotation (Anonymous, 1976). For *E. citriodora*, the same harvests in Brazil (Brandi et al., 1978) yielded 29 m^3 and 40 m^3/ha/year, respectively.

The yield of coppicing rotations may, however, be smaller than the seedling rotation due to failure of many stumps to produce coppices or to subsequent death of the coppices. In Brazil, Brandi et al. (1978) reported, respectively, for *E. botryoides* and *E. kirtoniana* reductions of 25 m^3 and 17.6 m^3/ha when seedling rotation was compared to the first coppicing rotation.

Utilization and Important Wood Properties

Variation in wood quality depends on differences at the cellular level in the chemical composition and ultrastructural and microscopic character of the wood. Substantial variation also occurs at higher levels of organization as, for example, interspecifically. Because of the large number of species, it is possible to select one or more

species of eucalypts that, within certain limits, will serve many purposes.

Eucalypt species can be utilized for a large number of purposes such as fuelwood, pulpwood, charcoal, small poles, posts, sawnwood, railway ties, veneers and plywood, and essential oils. However, the yield from the 3.7 million hectares of eucalypt plantation may be divided roughly into fuelwood or pulpwood (85%), poles and roundwood products (10%), and sawnwood (5%) (Anonymous, 1976).

The ranges (Hillis, 1978) in some wood properties of eucalypts important for their utilization are: cellulose 40 to 62%, hemicellulose 12 to 22%, lignin 15 to 22%, ash 0.1 to 0.6%, fiberlength 0.45 to 1.6 mm, and density 300 to 1,000 kg/m^3. Eucalypts have relatively low calorific values which vary from 4,700 to 4,800 calories/kg of dry wood. The wood when carbonized to charcoal yields about 7,900 calories/kg.

In many countries eucalypt plantations have been used to produce charcoal. Approximately 0.7 tons of charcoal are burned in blast furnaces to make one ton of charcoal iron (Anonymous, 1976). Alternative uses of charcoal include the production of domestic gas, fuel for motor vehicles, industrial chemicals used in paint industries, fireworks and gun powder, and rubber production.

The use of eucalypt for pulping is extensive in several countries. Some species of eucalypts provide a very good short-fiber pulp but others are less suitable. In general, species with denser wood have thick-walled fibers which do not make strong paper. To produce the better grades of paper, eucalypt pulp must be mixed with long-fiber pulp.

The timber of *E. grandis* is lighter, softer, and more fissile than that of most eucalypts. It is extensively used for house construction in Australia and the young material is suitable for case timber and for pulp and paper. The heartwood portion of the trunk is reddish brown, moderately hard and has an average basic density of 600 kg/m^3 (Turnbull and Pryor, 1978). The wood has moderate strength and durability, straight grain, but it is coarse in texture.

As with most eucalypts, fiber length, diameter, and wall thickness of *E. grandis* increase with age and position in the tree. In fast-grown trees of this species (Hillis, 1978), the fiber length increased from 0.69 to 1.05 mm from the pith to the periphery in the region between 0 and 12 cm from the pith and the maximum length was found at a height of 8.0 m from the ground. The fiber diameter also increased from the pith to the periphery in 15-year-old trees. The largest diameters were found at 10.7 m above ground level and the smallest at the top of the tree. The thickness of the fiber wall, which contributes to the strength of the wood, its machinability, and various pulp and paper properties, is closely related to density in this species.

Assessment of Site Quality

Site quality can be assessed and expressed in several ways depending on the conditions of the forest and objectives for which it is sought. Evaluation of the various methods of site quality estimation has been performed in detail by several authors (Carmean, 1975, 1977; Jones, 1969; Pritchett, 1979; Rennie, 1963).

Expression of Site Quality

Tree growth is a feature of the forest that is of special interest to foresters and it is important to consider site quality in terms of this feature. Ideally, site quality should be expressed in terms that best indicate the amount of material usable for a particular purpose. That is the case, for example, when the purpose of the forest is pulp, for which weight of wood rather than volume could best be used as a measure of productivity. Other alternative methods for expressing site quality include various aspects of wood quality, yields of resin, tannin, or cork per hectare (Rennie, 1963); or calorific equivalents of wood (Ralston, 1964). However, most of these measures have not been used frequently in site quality evaluation because of the complexity of their determinations or because they may be affected by factors other than those of the site. For example, the use of volumetric and weight yield tables is limited because of their dependence on accurate delineation of stand density effects (Ralston, 1964).

In most studies of site quality evaluation, some measures of stand height have been adopted. Theoretically, height growth is sensitive to differences in site quality, relatively free of stocking effects, species composition, and strongly correlated with volume. The most useful and widely accepted indicator of site quality is site index, which is the mean height of the dominant and codominant trees in relation to their age. Other indicators of stand height are the total height of dominant and codominant trees, mean annual height increment, and growth intercept index.

Methods for Estimating Site Quality

The methods for estimating site quality can be grouped in several ways but the simplest one is to divide them between methods that measure some characteristic of tree growth considered sensitive to site quality and methods that measure tree growth together with some other related attribute to the habitat. In the first group, the forest growth itself serves as the criterion of site quality and the methods are called "direct" methods. In the second group of methods, the attribute is the criterion, i.e., they are "indirect" methods and their reliability depends upon valid relationships between the attributes of the environment and tree growth. However, regardless of the ultimate method used to evaluate site quality, the initial determinations are made from direct measurements of some attribute of tree growth.

Direct methods

Site index. Site index is the term used to express the height of free growing, uninjured, dominant, or dominant-codominant trees of a stand projected to some particular index age. In the United States, the index age of 50 years has been adopted for most species (Spurr and Barnes, 1973). Younger index ages should be used for fast-growing species or for species managed on short rotations while older ages (100 years for example) may be desirable for some slow-growing species.

The accuracy of the site index method depends on the presence of suitable trees for measuring site index and on the availability

of accurate site index curves or tables (Carmean 1975, 1977). Thus, once site index estimates for a particular species are obtained, they are related to the curves or tables that predict growth and yield for different stand ages and for different levels of site index.

For years, the standard method of site index curve construction in the United States was the graphical anamorphic method (Jones, 1969). Construction of curves assumed that all factor combinations sampled produced height-age curves which were harmonic, i.e., were proportional to each other throughout the ages of the stands, and that a site index given by any stand would not change during the life of that stand. As pointed out by Carmean (1975), this assumption is not valid and height growth patterns are polymorphic for most species that grow on contrasting sites or that have a wide geographic distribution. Diversity in the forms of height growth curves is assumed to be caused by different combinations of site factors and changes in the identity of limiting factors during stand development. A good example of those types of changes was given by Pritchett (1979) for slash pine growing on the wet savanna soils of the southeastern United States. Under these conditions slash pine grows quite slowly in the first 10 to 20 years, but its rate of growth increases subsequently as the water table is lowered resulting, therefore, in larger exploitable volumes of soil with improved conditions for nutrients and aeration.

Alternative means of improving the accuracy of site index curves include stem analysis, internode studies, and height-growth records from permanent plots. The first two techniques are suitable for species which present annual rings or those having noticeable limb

whorls marking the course of annual height growth. For species growing in more tropical regions, permanent plots are necessary.

The major drawback of using site index as a direct method of site quality evaluation is that it cannot be used for sites devoid of trees or those lacking suitable trees. Furthermore, age of trees must be known, and this is in many cases difficult or impossible to determine.

In many stands, suitable dominant and codominant trees of other species may be present, but not usable trees of the desired species. For such stands, tree species actually present can be used for estimating site index and then the site index evaluated for the desired species by comparison. Graphs or equations previously constructed relating the site indexes of the two species are used for that purpose (Carmean, 1975). Although this method may be the only recourse available in some instances, it presents the disadvantage of compounding errors initially made in establishing the base equations or graphs. Another problem of this method is that the two species may present different growth patterns with age. Thus, a reasonable range of ages may have to be considered when constructing the graph or regression equations relating the site indexes of the two species.

Growth intercept. With the attempt to minimize the effects of irregularities during the establishment period and to provide a means for identifying growth differences in young stands, Wakeley and Marrero (1958) proposed the growth intercept method. This method uses as an index, the height growth of an early period of the stand, usually the five year period after the tree reaches the breast height level.

The method is useful for young trees of species which produce clear annual internodes and particularly recommendable for species managed for short rotation periods. The reliability of the method for species under long rotation systems is doubtful because early growth intercept measurements may not be a very good indicator of height growth in later years. Furthermore, the method is not reliable for species which do not produce annual internodes or produce more than one internode during a single growing season.

Indirect methods

Plant indicators. The concept of using plant communities as indicators of site quality was proposed before 1892 and elaborated on in Finland by A. K. Cajander and in Russia by G. F. Morosov (Daubenmire, 1976). It is assumed by this method that the understory plant species are integrators of the site features important for tree growth and thus useful indicators of forest site quality. The method involves first a classification of vegetation in terms of presence, abundance, constancy of occurrence, and size, with each type then calibrated against growth of existing stands. For a species to be a good indicator of site quality, it should tolerate very narrow ranges of ecological conditions.

The plant indicator method has been successfully used in undisturbed forests in northern regions because they usually have relatively few understory plant species and plant communities are usually distinct and easily recognized (Carmean, 1975). In regions where the forest is a more complex system, as is the case of forests of lower latitude regions, the method is more difficult to be applied

and the indicator plant spectrum was proposed by Spurr (1952). In this case site quality is estimated by assessing the presence and abundance of key species ranging from the poorest to the best site indicators.

The plant indicator method was subject to criticism by several authors (Coile, 1938; Lutz and Chandler, 1946; Viro, 1961), but according to Daubenmire (1976) the failures of the method are often obvious in the techniques adopted by the researchers and include small size of samples, unstable stands, and laboratory techniques used. Coile (1938) questioned the usefulness of the method when it is applied to severely disturbed systems and wondered whether shallow-rooted ground vegetation would reflect the deeper lying soil conditions explored by tree roots. In addition to that, the composition and vigor of the understory vegetation may be affected by the density and type of species of the overstory layer. The absence of the key indicator species during dormant seasons would also restrict the application of the method to certain months of the year.

Despite those limitations, plant indicators can be helpful when used in conjunction with other site evaluation methods for delineating and stratifying more homogeneous sites.

<u>Synecological coordinates</u>. This method was developed by Bakuzis (Jones, 1969) for forest classification in Minnesota and it is based on the ranking of factors such as moisture, nutrients, light, and heat requirements of forest plants ranging on a scale from 1 to a maximum of 5. Ecographs are then prepared and tree and site features related to paired coordinates from these various ratings. In most

cases the ranking is subjective and arbitrary and constitutes the major shortcoming of the method. Reliable rankings can be obtained when based on research where measures of site quality are correlated to determined values of moisture, nutrients, and other soil properties. However, in this case it is preferable to use multiple regression procedures which permit a more complete analysis of the complex relations of the site factors than simple correlations or pairing of selected site factors.

Physiographic site classification. The most widely used method of physiographic site classification was developed by Hills who introduced the concept of "total site" classification (Jones, 1969). Total site is defined as an integrated complex of climate, relief, geological material, soil profile, ground water, and communities of plants, animals, and man. It stresses, therefore, the holistic concept of site and physiographic features are used as the framework for integrating and rating climate, moisture, and nutrients (Spurr and Barnes, 1973).

Carmean (1977) argued that the broad ecological viewpoint of the method differs from the specific point of view of site quality in which quantitative measures are used for classifying forest land productivity. Like the synecological coordinates method, the physiographic method involves subjective and arbitrary ratings and the close and mutual dependence of the various factors at all levels make the application of this system difficult (Jones, 1969; Carmean, 1975). It is, however, useful for stratifying inaccessible forest regions into broad subdivisions based on general features of climate, topography, soil, and vegetation.

Soil survey. The taxonomic units of soil maps can constitute a good tool for site productivity appraisal. While this is true for the most recent soil surveys, old soil surveys were concentrated and detailed only for those pieces of land more suitable for agriculture crops. Generally, lands destined to forest plantation are undesirable for agricultural purposes due to physical, chemical, or physiographic limitations. Many of the modern soil surveys have been prepared and interpreted in such a way as to provide indications on alternative uses of the land, including forestry. Furthermore, in recent years, specific forest soil surveys and forest inventories have been performed by forest industries and public agencies. In any case, the reliability of the survey mapping units for estimating forest site quality will depend on the relationships of the unit classifying criteria with the important features dictating tree growth. Stoeckeller (1960) found soil surveys to be reliable for estimating site quality but other studies (Carmean, 1961; Phillips and Markley, 1963; Shetron, 1972) showed that site index varied widely within each soil mapping unit. Probably much of the site variations within soil units are due to variations of certain soil and topographic features such as thickness of surface soil, aspect, slope position, etc., which are important for tree growth but are not well described in the soil unit definitions (Carmean, 1975). Nonetheless, soil surveys constitute an excellent starting point for site quality evaluation; knowing the important variables affecting growth of the desirable forest species, refinement of the soil survey maps can be made, thus providing a reliable means for site quality estimation.

Soil-site evaluations. The soil-site methods take into consideration climatic, edaphic, and topographic features for predicting tree growth (site quality). Generally, for small regions, where only minor micro-climatic effects occur, edaphic and topographic variables explain most of the variation in tree growth. The effects of topographic factors are usually indirect, being reflected on tree growth through some soil properties. Thus, soil is of paramount importance in determining site quality in defined areas. Usually, soil properties more closely related to growth causative factors, i.e., moisture, aeration, and nutrients, have been found to be most important in soil-site studies (Coile, 1952; Carmean, 1975).

The soil-site method is particularly useful for areas where no direct estimation of site quality can be performed, either because trees are not suited for direct measurements or for areas with great variations in soil and site characteristics. Usually, equations relating some measure of tree growth to soil-site features are established by multiple regression analysis and used for calculating tables or graphs for estimating growth index in the field. In developing the equation, preference should be given to those variables easily determined in the field and in the laboratory. Equations including variables which require expensive or sophisticated equipment for their determinations are of little practical interest.

Extensive reviews including soil-site studies in the United States were performed by Coile (1952) and Carmean (1975). From these reviews it appears clear that soil texture, soil depth, stone content, slope position and steepness, and drainage are among the most important features affecting tree growth.

The relative importance of soil-site features in predicting site quality may vary or differ according to tree species, soil, topography, and climate of the area. Thus, results are valid only for the particular study area and for the soil and topographic conditions sampled within the study area.

The soil-site method was successfully used for predicting height growth of *E. alba* in Brazil (Barros, 1974), where for homogeneous areas of Latosol, slope steepness and content of P and Al in the soil were found to be the most important variables. However, for more heterogeneous areas with associations of podzolic and poorly developed soils, thickness of the B horizon, and contents of clay, P, and organic matter were the most important site factors. For this heterogeneous area, better equations were obtained when the data were subdivided by soil types. In Australia, McColl (1969) was able to indicate the best sites for growth of six species of eucalypts based on soil-site characteristics. *Eucalyptus gummifera* presented best growth on ridge sites with a high content of Al but low in P, Ca, Mg, and K; *E. maculata, E. paniculata*, and *E. pilularis* grew better on slopes where soil was medium in those elements; while *E. saligna* preferred gully sites where soil was low in Al, and high in P, Ca, Mg, and K.

Most of the successful soil-site studies explain 65 to 85% of the variation of tree height, or site index, observed on field plots (Carmean, 1975). The precision can be improved by stratifying the area, subdividing plot data for separate analysis, and including in the regressions as independent variables features causing great variability. If these features are not numeric variables, the subdivision of the

data is the only recourse that can be used for improving the precision. Another measure that helps improve the prediction equations is to assure that an adequate number of site plots are established so as to properly sample the full range of the defined soil, climatic, and topographic conditions within the study area (Carmean, 1975). The proper description of the relations between site quality and site features depends on an adequate sampling of average conditions as well as an adequate representation of extreme conditions.

Proper mathematical treatment of the data also plays an important role in the precision of the equation in predicting site quality. This has been met more easily with the advent of digital computers and subsequent computer programs which permit a more complete analysis of the data allowing the test of non-linear relations and interactions between variables. Relations between site quality and features of soil and topography are often curvilinear instead of linear as implied by many older soil-site studies (Carmean, 1975). The present computing facilities, however, have not made earlier soil-site regressions obsolete as demonstrated by Wright and Van Dyne (1971).

From the statistical point of view, the success of the regression equations has been indicated by two parameters: the coefficient of multiple determination (R^2) and the standard error of estimate (SEE). It may happen, however, that equations with good values of R^2 and SEE, are poor in predicting site quality in the field because soil-site results apply only to the particular area studied. Examples of good accuracy (Graney and Ferguson, 1971) and failure (Broadfoot, 1969; McQuilkin, 1976) of equations to predict growth are found in the literature.

Carmean (1975) stated that site index is a better dependent variable than tree height because the R^2 value is a better estimate of the site quality variation explained by the independent variables of soil and topography.

In trying to interpret established regression equations, one should keep in mind that in many cases the soil and topographic characteristics are not completely independent of each other and may be closely correlated, conditioning the trends in site quality. Because of the empirical nature of the regression equations established in soil-site studies, it is often difficult to give a biological or physiological interepretation to the observed effects of the variables on tree growth, i.e., the correlated factors need not to be causative factors. In any case, the major objective of this type of study is to obtain means for estimating site quality for the study area.

Factors Affecting Site Quality

Tree growth is determined by tree inherent factors and environmental factors. Of the environmental factors, the biotic components are more transitory and more easily managed by man than the abiotic or physical components. However, in measuring site quality, both components have to be taken into consideration.

Biotic Factors

The biotic factors can affect site quality by two manners: a) they can directly reduce growth, and b) they can constitute sources of errors in measuring growth effects of site variables (Ralston, 1964). The major biotic factors are genetic variation, stand density, competing vegetation, and insects and diseases.

Genetic variation

Differences in productivity between species growing on similar sites are well known by foresters and can readily be assessed. However, identification of hereditary variation in growth rate within a species complex is more difficult and, in most cases of site evaluation, it is included as a portion of the experimental error (Ralston, 1964).

The recognition that genetic variations affect tree growth has been a reason for many studies with the objective of yield improvement through selection and breeding (Pritchett, 1979). Intra- and inter-specific growth variations for species growing on the same site have been reported (Gomes et al., 1977; Shetron, 1972). Provenances and species of eucalypts presented different rates of height growth when planted on a same soil type in southern Brazil (Gomes et al., 1977). For example, the differences in height and diameter growth between the best and the poorest provenances of *E. grandis* were 20% and 10%, respectively.

Stand density

Height of dominant trees is considered to be relatively free of the effects of stand density. However, it is important to the growth and survival of intolerant species (Pritchett, 1979). In addition, as stated by Ralston (1964, p. 176), "inadequate density of desirable growing stock is perhaps the most important single factor limiting potential forest production on millions of otherwise reasonably productive acres."

Meskimen and Franklin (1978) reported that the merchantable volume and height of 7.4 year-old *E. grandis* plantations in southern Florida were about the same whether the number of trees per hectare was 2867 or 715 but the total volume was 1.7 greater in the denser stand.

Competing vegetation

Undesirable vegetation competes with forest species for growing space, light, moisture, and nutrients, consequently reducing forest productivity. Competition from both ground and overstory vegetation can be a very important factor affecting survival, establishment, and growth of planted forests. Eucalypt species are very sensitive to competition during their first years in a plantation. Usually good site preparation helps in the control of weeds and, if the site is not very infested, one or two weedings in the first year of the plantation is sufficient for weed control. This would permit the eucalypt canopy to close and shade the understory vegetation.

The weeding methods to be used depend on the topography of the area. Where possible, the weeds can be removed by disking between the rows and hand-pulling or hoeing near the trees. In Brazil, Brandi et al. (1974) tested three manual weeding methods and their combinations to control *Imperata brasiliensis* (blady grass) and *Melinis minutiflora* in plantations of *E. alba, E. botryoides,* and *E. saligna.* Weedings were performed five times with two of the weedings in the second year. The best weeding treatment consisted of complete hoeing of the plot; the trees in plots receiving this treatment were three times taller than those of the control plot (no weeding) at the end of 27 months. Competition for nutrients and moisture was

presumably the reason for the reduced rate of growth in the control plots because hoeing applied to a radius of 40 cm from the seedlings resulted in a doubling in height.

Very little information is available on the use of chemical weed control in eucalypt plantations. Some preliminary studies (Cremer et al., 1978) showed that eucalypts are susceptible to the phenoxyacetic acids. *Eucalyptus regnans* was tolerant to simazine and propazine at rates up to 16 kg/ha of active ingredient but susceptible to atrazine.

Diseases and insects

Intense attacks of insects and diseases appreciably reduce tree survival, growth, and yield. Failure in detecting such injuries may result in biased site quality measurements. Pritchett (1979) cited examples of drastic reductions on pine productivity due to occurrence of such diseases as *Fommes annosus* and *Cronartium fusiforme*.

Several diseases are known to attack eucalypt species but their effects on yields have not been determined. Diseases are known to attack leaves (*Oidium eucalypti*, for example), stems and branches (*Diaporthe cubensis*), roots (*Armilaria mellea*), and heartwood (Basidiomycetes) (Anonymous, 1976). In Brazil, the incidence of canker caused by *D. cubensis* on eucalypts may reach 80% of the trees in the case of more susceptible species. For *E. grandis* plantations in southern Brazil, the incidence of canker appears to depend on seed sources reaching about 60% in the more susceptible provenances.

Insect attacks can significantly reduce the productivity of eucalypt plantations. Large numbers of defoliating and sap-sucking

insects have been reported to attack eucalypts (Anonymous, 1976). In most cases, insect attack occurs occasionally but frequent attacks from termites and highly organized colonies of ants are common. Soil termites represent a serious hazard to eucalypts planted in some subtropical and tropical areas particularly in the initial year or two after planting. The leaf-cutting ants of the genus *Atta* and related genera are the biggest enemies of eucalypt plantations in South America. In Brazil, it is virtually impossible to establish eucalypt plantations, or, if established, the plantations will not be productive if ants are not controlled. The importance of ants as a biotic factor in site productivity in Brazil can be summarized in the following statement: "Should eucalypt plantations be abandoned as production units in north-central Brazil, it is quite likely that large sections of them would disappear as eucalypt stands because the *Atta* ants would destroy all the regeneration" (Anonymous, 1976, p. 175).

Abiotic Factors

Tree growth as a response to physical or abiotic factors of the environment is usually much easier to be observed and demonstrated than as a response to biotic factors. The abiotic factors to which tree growth has been more closely correlated were reviewed by Carmean (1975), Coile (1952), Pritchett (1979), and Ralston (1964). These factors have usually been grouped into climatic, topographic, and edaphic variables.

Climatic variables

Generally the effect of climatic variables on site quality can only be noticed on relatively broad regions. Changes in climate are usually followed by changes in the types of vegetation. However,

topography can cause changes in climatic variables in relatively small areas. Thus, the amount of rainfall, for example, on one side of a mountain may be high but low on the other side because of physical impediment provided by high mountains for cloud movement.

Indices relating climatic variables with potential forest productivity were developed by Weck and Paterson, as cited by Ralston (1964), based on combined effects of temperature amplitude, length of growing season, precipitation, and solar radiation.

A well-known study of site productivity in which climatic variables were of great importance was that carried out by Jackson (1962). He studied growth of slash pine plantations located in Australia, New Zealand, and the United States and found that the mean annual height increment increased with rainfall when other variables were kept constant.

Matching Brazilian climatic conditions, by the Thornthwaite hydraulic balance method, with those of the sites where eucalypts are native, has proved to be a valuable indicator for selecting species potentially capable of growing well in the various Brazilian regions.

Topographic variables

Topography is closely related to differences in microclimate, soil development, and soil nutrient regime, and consequently a good indicator of site quality. Topographic features can be treated as indicator variables such as ridges, slopes, coves, and bottoms or they can be regarded as measurable characteristics such as gradient, altitude, and aspect. Stratification of the site based on topographic characteristics may provide a means for a better precision in

estimating site quality (McQuilkin, 1973). However, excessive detail in topographic classification may lead to errors (Ralston, 1964).

Increases in slope percent usually reduce tree growth (Myers and Van Deusen, 1960; Zahner, 1958) but opposite results have also been reported (Bowersox and Ward, 1972; Della-Bianca and Olson, 1961). In Brazil, slope percent negatively affected yield of *E. alba* growing on a Latosol and accounted for 88% of the variation in height (Barros, 1974).

Aspect is another topographic feature frequently reported as an important factor affecting site quality particularly in mountainous areas and cold climates. The effect of aspect on growth of oaks in Arkansas and Indiana was reported by Graney and Ferguson (1971), and Hannah (1968), respectively.

As for the effects of topographic variables on growth of *E. grandis* little is known. In its natural habitat, *E. grandis* normally occurs in moist gullies but it is found on tablelands in northern Australia (Turnbull and Pryor, 1978).

Edaphic variables

Besides biotic, climatic, and topographic variables, soil is the remaining factor of the environment that significantly influences tree growth. Variations in tree growth within a homogeneous topographic class are frequently associated with differences in available supplies of water, or soil atmosphere, or soil nutrients (Ralston, 1964). Thus, soil properties affecting moisture, aeration, and nutrients in the root zone are usually related with site quality.

Specific studies on soil requirements of many of the eucalypt species are yet to be done. However, it is presumed that most species respond to planting on deep soils of moderate fertility and good texture and structure. Although the level of acceptable fertility is a good deal less than for agriculture crops, it is more than that required for many of the pines (Anonymous, 1976). Responses to fertilizer application depend on local soil conditions but there are reports of large responses, particularly to N and P fertilization (Barros, 1977; Schutz, 1976).

Soil depth. Soil depth is of major importance for tree growth. Quantity and quality of growing space for tree roots can be an indirect measure of available soil moisture, fertility, aeration, and microbial activity. Soil depth is particularly important in sites where root growth is limited by such restricting layers as claypans, hardpans, bedrocks, or other horizons of low permeability that define the effective depth of the profile. In addition, the effective depth can be defined by high water tables or presence of toxic substances.

Usually tree growth is more affected by shallow soils than by deeper ones and growth shows a reciprocal trend when plotted against depth. Zahner (1958) found a quadratic relationship between surface soil depth and site index of loblolly and shortleaf pines growing on zonal soils of Arkansas and Louisiana. Site index of both species increased with increasing depth of the soil to a maximum at about 46 cm then decreased with further increases in depth. Decrease in growth as affected by soil depth usually reflects deviations from

good conditions of soil moisture and aeration for tree growth. Soil texture and topography tremendously affect these conditions. In results described by Zahner (1958), the decrease in site index for depths beyond 46 cm was a consequence of the excessive drainage provided by the subsoil. The fine textured surface of shallow soils overlaid subsoils with a high content of silt-plus-clay and the aeration was poor. Site index of black oak on slope sites was found (McQuilkin, 1973) to increase with B_2 depth for soils with high amounts of sand in the B_2 but decreased for soils with low sand contents in the B_2. For the top-ridge sites, deep soils provided better site-index than shallower soils, particularly when associated with clay soils. Row (1960) found that site index of slash pine planted in the sandhill region of the Carolinas increased with depth of the A_1^* horizon but decreased when the depth to the fine textured horizon was greater than 25 cm.

Linear trends between growth and soil depth generally occur when the range of moisture-aeration conditions which affect the growth of the species is only partially represented by the sample plots. Coile (1952) and Zahner (1954) declared that the net effect of increasing depths of the B horizon and the subsoil was increased growth of slash pine. In the Atlantic and Continental regions of Canada, the direct relation between site index of black spruce and rooting depth reflected better drainage conditions provided by medium to fine-textured soils (Lowry, 1975).

Few species of eucalypts will grow well on very shallow soils, although some can take advantage of fissures in the underlying rock to maintain stability and obtain nutrients (Turnbull and Pryor, 1978).

Positive correlation between rooting depth and height of *Eucalyptus alba* was found (Barros, 1974) for a mountanous area in Brazil in which a high percent of rock fragments was present. High percentages of rock fragments close to the soil surface affected water availability and soil nutrient regimes reducing height growth.

Depths to fine-textured layers and mottling have been reported as important soil factors affecting site productivity (Barnes and Ralston, 1955; Linnartz, 1963; Pegg, 1967; Ralston, 1951; Shetron, 1972), and its increase is often related to better nutrient and aeration conditions. For sandy soils in Florida, Barnes and Ralston (1955) reported that site quality for slash pine increased as depth to a fine-textured horizon and to mottling increased, reaching a maximum at about 75 cm and 90 cm, respectively. Site quality gradually decreased with further increases in both properties. Similar results were reported by Linnartz (1963) and Pegg (1967) with respect to depth of soil layers of low permeability for loblolly and slash pines, respectively.

In Israel, Karschon and Van Praag (1954) found that growth of *E. camaldulensis* was positively related to depth to a hardpan and the best growth occurred at depths nearing 110 cm. Gilmore et al. (1968) reported that depths to a fragipan explained 90% of height variation of yellow poplar.

Depth of tree rooting was closely related to soil drainage classes in a study performed by DeMent and Stone (1968) in red pine plantations in New York. Maximum growth was observed on soils with moderate to well drained regimes where the depth of tree rooting was about 110 cm. Tree growth was adversely affected by fragipans or bedrocks

at shallow depths in soils with impeded drainage and by the high water table on the poorly drained soils in which it persisted in or near the surface layer for long periods. On the excessively drained soils, tree growth was reduced because the soil was very deep (more than 125 cm), coarse textured, and marginal in terms of fertility and moisture storage capacity.

The role of chemical layers in determining the effective depth for growth of eucalypt roots was shown by Kaushik et al. (1969). The combined effects of claypan and a layer high in calcium carbonate or in salt content were detrimental to growth of eucalypt roots in two regions in India. Calcium carbonate was partially responsible for almost complete failure of the plantation when present as indurated pans. The plants also could not thrive on soils with a content of soluble salts greater than 0.7%. The minimum limit for salt injury on *Eucalyptus* hybrid was found to be 0.15%.

Soil texture. Texture is a soil property that has been related to tree growth since early studies (Coile, 1952). Soil texture has often been reported as the factor more closely related to supply of water and, in many cases, as an indicator of soil aeration. As it is true for any measurable soil property, the effect of texture may range from a beneficial, to nil, to a detrimental effect on tree growth.

The increase in finer fractions in a soil dominated by coarse fractions such as gravel and sand may be related to tree growth because of improved moisture retention conditions; on the other hand, the increase of coarser fractions in a soil dominated by fine fractions may influence growth because of better aeration. This general pattern

can be modified by soil structure, presence of impermeable layers, and topography.

In several studies (Barnes and Ralston, 1955; Bowersox and Ward, 1972; Phillips and Markley, 1963), the increases in silt and clay contents were associated with increases in tree growth but inverse relations were found in other studies (Broadfoot, 1969; Hannah, 1968; Jackson, 1962). In the latter cases, aeration was frequently found to be deficient and increases in the sand fraction favored tree growth.

Zahner (1958) found that on zonal soils site index of loblolly and shortleaf pines increased as the clay content of the subsoil increased to a maximum of 25% and 35%, respectively, whereupon additional increases of clay resulted in reductions of site index. On azonal soil groups, similar relationships were found between site index of loblolly pine and silt-plus-clay content of subsoil but an increase of silt in the surface soil linearly decreased site index.

Barnes and Ralston (1955) reported that water retention was closely related with silt and clay content of soils in Florida, particularly in sandier soils. The correlation of growth with percent of these fine materials in the profile was positive; site index of slash pine increased until the silt-plus-clay content reached about 12% and then practically leveled with further increases of these fractions. Similar results for red pine were reported by Wilde et al. (1964b) for non-phreatic sandy soils in Wisconsin.

Increase in sand content in the B_2 horizon of slope sites (McQuilkin, 1973) improved site quality for black oak in southeastern Missouri while high content of sand in the A horizon decreased growth.

Linnartz (1963) reported that in Louisiana the effect of sand content of the subsoil on site index depended on the tree species and the depth to the least permeable layer. For loblolly and longleaf pines, site index increased as the content of sand of the subsoil decreased but for slash pine, increases in site index were associated with increases in sand content of the subsoil, as long as the topsoil was not very sandy or the least permeable layer was not very deep in the profile.

Soil texture was the most important soil factor in predicting growth of sweetgum stands on mature soils in New Jersey (Phillips and Markley, 1963). Clay and fine sand in the B horizon accounted for about 50% of growth variation. Site index increased linearly with clay content but its relation with fine sand was linear to a maximum of 45% fine sand and declined thereafter.

Increases in sand content positively affected height growth of *E. alba* growing on a Latosol in Brazil but it was detrimental to growth of the species on younger soils in a mountainous area. In the first case, the increase in sand presumably improved aeration in those plots located in low-slope and bottomland sites, whereas in the mountainous area the increases in finer particles resulted in greater soil water retention capacity.

Yadav and Prakash (1969) reported that growth of a *Eucalyptus* hybrid in India was adversely affected when the soil had coarse texture with an excessively bouldery subsoil having a deficient moisture supply. Growth was better on soils with a silty loam texture and associated with a somewhat higher water table.

Water table and soil aeration. The presence of shallow fluctuating water tables is an important soil factor affecting forest growth in the lower coastal plain of the United States. Large cyclical variations in water tables are undesirable because roots penetrating portions of the profile that become aerated during dry seasons are killed back by advancing water table during wet periods (Pritchett, 1979). This periodic root pruning phenomenon tends to create an imbalance in the root: top ratio and reduces the tolerance of trees to drought periods. Therefore, the depth to the water table in these poorly drained areas determines the effective depth of the soil during a large portion of the year. Water table, additionally, affects available soil moisture, soil nutrient availability, and drainage. The close relationships among depth to water table, soil air volume, and root growth of *Pinus contorta* were demonstrated by Boggie (1977).

Water table may also influence the uptake and distribution of nutrient elements due to both biomass changes and the larger soil volumes exploited by the more extensive root systems (White and Pritchett, 1970).

Phillips and Markley (1963) argued that the use of water table data to predict site index seem impractical. The needs for frequent measurements and the possible differences in the depth of the water table and mottling within and between growing seasons were the major obstacles pointed out by these authors. Depth to water table also may be considered a transitory characteristic in site evaluation because it usually increases as trees increase in size and transpire larger quantities of water.

Water table depth was shown to significantly affect tree growth in several studies. White and Pritchett (1970) found that growth of slash and loblolly pines on Aquods was better on plots with water table controlled at 46 cm than on plots with a water table at 92 cm or where it was permitted to fluctuate naturally. Similar results were reported by Gresham and Williams (1978) for loblolly pine in South Carolina. The best growth occurred when the water table depth was about 70 cm and it decreased as depth increased beyond this point. Phillips and Markley (1963) reported that growth rate of sweetgum was also affected by both average water table depth and amount of fluctuation during the growing season. The best growth was found when the water table was relatively constant at depths of about 50 cm; the poorest growth was observed when the water table was shallower and fluctuated widely during the growing season.

A relative indication of the depth of the water table is provided by drainage classes. The relation between growth and drainage classes is usually curvilinear with a well-defined maxima at moderately and well-drained classes which presumably represent optimal moisture and aeration conditions. The relation between drainage classes and growth was curvilinear for red pine (DeMent and Stone, 1968), positive and linear for radiata pine (Ballard, 1971), and negative for both white pine (Mader, 1976) and red pine (Mader and Owen, 1961).

In the lower coastal plain, shallow water tables, besides being influenced by the generally low altitude and flat topography of the area, are also greatly affected by the presence of impermeable soil horizons. On these sites, the spodic and fine-textured horizons of

low permeability may perch the water table and favor the development of poorly aerated conditions. In Florida, about 60% of the soils are either poorly drained, low-lying, or flat (Allen, 1977). Hence, they are subject to continuous, frequent, or intermittent waterlogging in all or a large part of the soil profile.

The adverse effects of waterlogging on plants are due to lack of O_2. Lack of O_2 in a soil horizon prevents root penetration and exploitation of nutrients and causes several important chemical and biological changes. The chemical changes are often brought about by biological redox processes resulting from O_2 depletion. The redox status of wetland soils determines the presence of toxic substances and the availability of several important plant nutrients (Patrick, 1978).

Extensive reviews on the relationships between plant growth and soil aeration (Allen, 1977; Grable, 1966) and soil aeration and chemical changes (Ponnamperuna, 1972) have been published.

Dissolved O_2 and pore space O_2 are usually depleted by soil microorganisms and respiring roots in about one day after the soil layer in which they are located is flooded. Land plants respond to O_2 stress in the roots by forming intercellular gas spaces in the cortex (Ponnamperuna, 1972). Limited amounts of O_2 may be transported from the shoot to the root cells through these spaces (Philipson and Coutts, 1978) to enable the plant to survive short periods of soil waterlogging. With time, however, roots become water soaked with the internal root air spaces and chambers filled with water. This condition decreases the rate of internal root aeration tremendously (Allen, 1977).

As with other plants, forest species vary in their resistance to waterlogging (Philipson and Coutts, 1978; Sanderson and Armstrong, 1978) and the resistance is linked with the capacity of the roots to oxidize the rhizosphere, presumably by O_2 translocation from the shoot (Ponnamperuna, 1972; Sanderson and Armstrong, 1978). Roots of some plant species also may carry on anaerobic respiration with the production of ethanol or other products that would otherwise by phytotoxic. Sanderson and Armstrong (1978) reported that acetic and butyric acids were highly toxic to Sitka spruce and lodgepole pine when applied to solution culture at levels reported to be found in paddy soils. The authors concluded, however, that the chief cause of rot root of these species was anoxia which preceded phytotoxin accumulation. The levels of C_2H_4, H_2S, and Mn (II) were very low and not responsible for root damage. Boggie (1977) found the relationship between O_2 concentration and weight of roots of *Pinus contorta* to be highly significant, particularly during those periods of greater O_2 restriction.

Lack of O_2 or metabolic inhibitors hinders or stops uptake of most nutrients or permits uptake of ions such as Na and Cl which are normally excluded by some species (Grable, 1966). Anaerobic condition may suppress growth of root hairs with a consequent decrease in nutrient uptake.

The relations among soil moisture, aeration, and nutrient absorption by slash pine seedlings were studied by Shoulders (1976) and Shoulders and Ralston (1975). Lowering the O_2 level in culture solutions from 90 to about 50% of equilibrium saturation with air, reduced the uptake of water, P, K, Ca, and Mg but increased uptake of NO_3-N.

Shoulders (1976) suggested that fertilization of poorly drained sites increased the concentration of nutrients in the soil solution, hence compensating for a reduction in the plant's efficiency for nutrient uptake.

White and Pritchett (1970) reported that the levels of nutrients in tree components of 5-year-old slash and loblolly pines were affected by water table control. For example, N and K foliar concentrations of trees growing in plots where the water table was maintained at 46 and 92 cm were higher than in trees in plots where the water table was allowed to fluctuate. The inverse was observed for foliar concentrations of Ca, Mg, Mn, and Zn, whereas P foliar concentration was unaffected. In another study involving a slash pine plantation, Kaufman et al. (1977) reported that drainage of a flatwood soil did not affect foliar concentration of any nutrient.

Of special significance to plant growth on waterlogged soils is the oxidation-reduction process involving N, Mn, Fe, S, and C. The reduction of these elements reflects changes in the microbial (bacterial) population from predominantly aerobic to anaerobic, starting when the redox potential of the soil reaches +330 mv (Allen, 1977). During anaerobic respiration, organic matter (electron donor) is oxidized and soil components (electron acceptor) are reduced. Hence, absence of O_2, presence of decomposable organic matter, and anaerobic bacterial activity are the requirements for soil reduction.

Oxygen is the first soil component to be affected and it is almost completely depleted in a day after the soil had been waterlogged. When O_2 drops to a very low level, nitrate is attacked; denitrifying bacteria and facultative and obligate anaerobes will predominate

between +225 and +330 mv. Nitrate is reduced to NH_4 and N_2. As a consequence, Mn, Fe, S, and CO_2 are reduced. Iron-reducing bacteria operate in the range of +120 to 220 mv, whereas S-reducing bacteria (Desulfovibrio) require much lower redox potential (-150 mv) to produce H_2S. Finally methane generating bacteria may produce CH_4 (Allen, 1977).

Oxidation-reduction processes also control the pH of most flooded soils. Usually waterlogging makes the pH values of acid soils (except those low in Fe) and alkaline soils to converge toward 7 (Ponnamperuna, 1972) although soil properties have strong influence on the pattern of the changes. Acid soils low in organic matter or in active iron slowly attain pH values less than 6.5. Acid sulfate soil low in Fe may not attain a pH more than 5.0, even after months of waterlogging. Grable (1966) cited authors who found the pH of acidic soils and soils containing high levels of organic matter that decreased when saturated.

According to Patrick (1978), the presence of an aerobic layer is the major cause of instability of N in a wetland soil and it results in considerable loss of N from the system by nitrification-denitrification reactions. Nitrate formed in the aerated layer diffuses downward into the anaerobic layer and undergoes denitrification. A similar process occurs in soils subject to fluctuating water tables.

Phosphorus is not directly involved in redox reactions in the soil but because of its reactivity with a number of redox elements, its behavior is significantly affected by waterlogging. Waterlogging generally increases the availability of P. Waterlogging of acid soils results in increased concentration of water-soluble P because (a)

hydrolysis of Fe and Al phosphates, (b) release of P held by anion exchange on clays and hydrous oxides of Fe and Al, and (c) reduction of Fe^{3+} to Fe^{2+} with liberation of sorbed and chemically bonded P (Ponnamperuna, 1972). The first two reactions are due to pH increases caused by soil reduction.

McKee (1970) studied the effect of fertilization and submergence on chemical properties of samples of an Aqualf supporting forest species. The redox potential decreased during submergence and was not affected by fertilization, whereas pH increased and was affected by the combined action of phosphate and lime applications. Submergence depressed the level of Ca and Mg but did not affect Na, K, and CEC. The levels of Al were reduced by submergence and liming and the dissociation was reduced at higher pH values. Submergence did not affect the level of total P but caused a decrease in Al-P and an increase in Fe-P. The process was supposedly dependent on pH. The decrease in Al-P was due to a decrease in the levels of exchangeable Al, while the increase in Fe-P was due to the presence of appreciable amounts of Fe in the soil. The author concluded that the effects of waterlogging on soil with marginal amounts of Ca, Mg, and P may render an appreciable portion of these nutrients unavailable, thus limiting tree growth.

Waterlogging can increase the availability of other elements such as Fe, Mn, S, Cu, Mo, Zn, and Co (Grable, 1966). Generally these elements interact with each other and may also form organocomplexes. However, when in high concentrations in the soil, they can cause plant toxicity.

Soil physical impedance. The presence of layers in the soil profile with high physical resistance to root penetration is an obvious factor affecting root growth and hence site quality. The strength of layers, other than rock layers, is affected by factors such as soil texture, structure, moisture conditions, and cementing substances.

In most cases, soil physical impedance to root growth is closely correlated to soil aeration and to soil drainage. In the lower coastal plains of the United States, root growth restrictions on Spodosols may result from impedance imposed by a cemented spodic horizon (Ortstein). This horizon occurs at different depths in the soil profile and shows wide variation in hardness. The effects of the spodic horizon on root growth in many sites in this region are difficult to separate from those of shallow water table (aeration) and of a fine-textured horizon that often underlies the spodic. Only careful examination of root morphology may help to differentiate these effects.

Studying soil resistance to root penetration usually involves two approaches: one consists of applying pressure to soil columns until obtaining certain values of bulk density and the other consists of the use of a penetrometer to measure soil strength. It has been shown (Barley et al., 1965; Blanchar et al., 1978) that bulk density and penetration resistance are closely correlated for the same type of soil and moisture content.

The effects of high soil density on growth of seedlings of seven tree species were studied by Minore et al. (1969) who used soil columns to which pressure was applied so as to provide bulk densities of 1.59, 1.45, and 1.32 g/cm^3. Seedling growth depended on the interaction species-bulk density; seedlings of western red cedar grown in columns

with bulk densities of 1.32 and 1.45 g/cm^3 were heavier than those grown in columns with a bulk density of 1.59 g/cm^3. Roots of lodgepole pine, Douglas-fir, red alder, and pacific silver fir penetrated soil with a density of 1.45 g/cm^3 which was too compacted for growth of Sitka spruce, western hemlock, and western redcedar roots. The increase in soil bulk density was reported to adversely affect site index of cherry bark oak (Broadfoot, 1969) and of mixed coniferous stands in northern Idaho (Brown and Loewenstein, 1978).

Measuring soil resistance to penetration and elongation of roots of agriculture crops has been a matter of concern of agronomists for many years. Studies have shown that both soil strength as measured by the penetrometer and bulk density are significantly related to root elongation of crops such as wheat and peas (Barley et al., 1965) and cotton and peanuts (Taylor and Ratliff, 1969). However, Blanchar et al. (1978) found that penetrometer measurements were better indicators in sandy soils than bulk density of root penetration and length. Fiskell et al. (1968) reported that morphological abnormalities of corn roots entering tillage pans of coarse-textured soils in Florida resulted primarily from soil strength impedance.

Root proliferation and elongation usually starts to decrease at relatively low values of soil strength, i.e., around 2 kg/cm^2 (Davidson and Hammond, 1977) but the point where growth no longer can be observed depends on the plant species. Taylor and Ratliff (1969) observed peanut root elongation into soils with resistance greater than 40 bars, although the rate of elongation was very low. Coultas (1973) reported that spodic horizon hardness ranging from 1.64 kg/cm^2 to 3.18 kg/cm^2 did not affect rooting depth and total root growth of loblolly and slash pines seedlings grown in the greenhouse.

Brandon et al. (1977) related soil strength and bulk density with brittleness of an undisturbed spodic horizon of a Leon soil (Aeric Haplaquod). Near field moisture capacity, non-brittle layers had hardness of less than 12 kg/cm^2. The hardness ranged from 12 to 24 kg/cm^2 in slightly brittle layers and was greater than 24 kg/cm^2 in brittle layers. Bulk density of the spodic horizon ranged from 1.4 to 2.0 g/cm^3 and no relationship between brittleness and bulk density was detected. Brittleness of the upper part of the spodic horizon was seen as a complete filling of the macropores by organic matter and silt particles. No other chemical or mineralogical differences appeared to be related to the consistence of the spodic layers.

Soil nutrients. In spite of the importance of soil nutrients to site productivity, only recent studies on forest production have given attention to the soil fertility factors. According to Ralston (1964), this lack of emphasis on fertility factors was due to the frequent close relation between soil nutrients and variables used to describe other soil properties and the difficulty in diagnosing fertility of forest soils. Furthermore, the conservative nature of nutrient cycling, deep-rooting habit, and mycorrhizal association (Pritchett, 1979) may prevent natural stands from showing nutrient deficiency symptoms. Disturbances to the stands may, however, affect the cycling process and cause decreases in growth. Cremer et al. (1978) reported growth responses to application of fertilizer by intermediate and small size trees in a naturally regenerated stand of 27-year-old *E. regnans* in Australia.

Several studies (Beadle, 1962; McColl, 1969; McColl and Humphreys, 1967; Parsons,1969; Parsons and Spetch, 1967) have indicated a close relation between soil nutrients and natural distribution of some species of eucalypts. Beadle (1962) reported that soil phosphate was the most important nutrient affecting the natural distribution of plant communities in eastern Australia. However, except for restricted conditions, distribution of natural stands cannot be related to a single factor because of interactions involving several other factors. McColl (1969) and McColl and Humphreys (1967) showed that the distribution of *E. gummifera* and *E. maculata-E. paniculata* association followed a sequence which was broadly related to gradients in soil nutrients and moisture status. The relative distribution of *E. incrassata* and *E. socialis* was found by Parsons (1969) to be controlled by slight soil differences with *E. incrassata* usually on soils both lower in nutrients and with higher water-supplying capacity.

Plantation forests involving exotic species, and even native species, provide an excellent means to indicate the dependency of forest productivity on soil nutrients. Eucalypt species have responded to fertilization in their native country (Cremer et al., 1978) as well as in countries to which they are exotic (Anonymous, 1976). Responses have been obtained more frequently to N and P fertilization (Barros, 1977; Cremer et al., 1978; Schutz, 1976) but on certain soils other elements such as K, Ca, and B also need to be added for good wood production.

In South Florida, growth responses have been obtained from operational application of rock phosphate and a recent study (Barros and

Pritchett, 1978) showed that application of N fertilizers significantly increased growth of a 4-year-old *E. grandis* plantation. The application of NH_4NO_3 at a rate of 200 kg/ha resulted in height and diameter increments 69% and 76% greater than the unfertilized control.

Soil nutrients have been included in the predicting equations in several soil-site studies. The content of P, Ca, and K in the A horizon, along with the content of organic matter of the B horizon, were the most important soil factors affecting height growth of *E. alba* in Brazil (Barros, 1974). McColl (1970) grew seedlings of *E. gummifera* and *E. maculata* in pots containing soil from 10 different sites and obtained best estimates for seedling growth with equations involving soil Ca and P. One or more of the soil mineral elements, i.e., N, P, K, and Mg, was reported to affect site quality of sweetgum (Broadfoot, 1969), loblolly pine (Nemeth and Davey, 1974), jack and red pines (Wilde et al., 1964a,b), red and white pines (Mader, 1976; Mader and Owen, 1961), radiata pine (Ballard, 1971; Raupach, 1967b), black spruce (Lowry, 1975), and *Cupressus lusitanica* (Fassbender and Tschinkel, 1974).

The increase of organic matter level in the soil has often been associated with higher productivity (Wilde et al., 1964a, b), but negative correlations have also been reported (Graney and Ferguson, 1971; Mader and Owen, 1961). Under wetland soil conditions, accumulation of organic matter is evidence of poor drainage and aeration and an inverse correlation of tree growth and organic matter content was, thus, observed (Ralston, 1964). Mader (1976) found that better sites for white pine had more organic matter in the B horizon but less in the A than average sites.

Soil aluminum and soil reaction. More than 15% of the earth's crust is made up of Al_2O_3 and thus Al is an important constituent of the soil. The solubility of Al is controlled by soil reaction and in neutral and alkaline soils the solubility of Al is too low to be toxic to plants. However, on acid soils with pH values below 5.0, the solubility of Al increases sharply and a great part of the cation exchange sites may be occupied by Al. Aluminum can be taken up by plants so that the detrimental effect of acid soils on plant growth is often due to high soluble Al levels rather than to high H concentrations.

Many Florida soils have appreciable amounts of exchangeable Al (Fiskell and Zelazny, 1971) which is the source of much of the active and potential acidity (Zelazny and Fiskell, 1971). The exchangeable Al is in equilibrium with Al ions in the soil solution. Active acidity (i.e., that measured by pH) is due to hydrolysis of trivalent Al (Blue and Dantzman, 1977) in the soil solution to form hydroxy-Al and H ions. Aluminum hydrolysis occurs in steps as follows:

$$Al^{3+} + H_2O \rightarrow Al\ (OH)^{2+} + H^+$$

$$Al\ (OH)^{2+} + H_2O \rightarrow Al\ (OH)_2^+ + H^+$$

$$Al\ (OH)_2^+ + H_2O \rightarrow Al\ (OH)_3 + H^+$$

The relationships of soil acidity-aluminum-plant growth were recently reviewed by Blue and Dantzman (1977) and Foy et al. (1978).

Spodosols may contain on the order of 0.1% of total Al as compared to 2 to 3% in Ultisols (Blue and Dantzman, 1977). The exchangeable Al in the surface soil is often relatively low, but it is the main cation in the spodic horizon comprising, in many cases, more than 80%

of the effective cation exchange capacity (Fiskell and Zelazny, 1971). The amount of Al in the soil solution necessary to cause plant toxicity is small and the problem becomes severe as the acidity increases to pH values below 5.0 (Blue and Dantzman, 1977). However, it is difficult to determine the potential for Al toxicity from a single measurement such as exchangeable Al. The percentage of Al saturation of the ECEC is another parameter that serves to indicate the relative amount of Al in the soil solution.

Aluminum often accumulates in the roots, leading to root damage and poor root growth. Root tips and lateral roots thicken and turn brown; many stubby lateral roots are present but with reduced fine branching (Foy et al., 1978). This deformation interferes with water and nutrient uptake, particularly that of P. Aluminum appears to reduce the solubility of P in the medium and restricts its uptake and utilization by plants (Foy et al., 1978). Hence, plants suffering from Al toxicity usually show foliar symptoms resembling those caused by P deficiency, such as overall stunting; small dark green leaves and late maturity; purpling of stems, leaves, and leaf veins; and yellowing and death of leaf tips. In other plants, Al toxicity appears as an induced Ca deficiency or reduced Ca transport problem, i.e., curling or rolling of young leaves and collapse of growing points or petioles.

Plant species and varieties vary widely in tolerance to excess Al in the growth medium. Aluminum tolerant plants must be able to prevent the absorption of excess Al or detoxify the Al after it has been absorbed (Foy et al., 1978). McCormick and Steiner (1978) tested

six genera of trees to 10 different levels of Al applied to hydroponic growth medium and reported that *Populus* hybrid and *Elaeagnus umbellata* were very sensitive to low Al concentrations (10 to 40 ppm), whereas *Alnus glutinosa, Betula* spp, *Pinus* spp, and *Quercus* spp were tolerant to much higher concentrations (80 to 160 ppm).

Plant physiological factors related to Al tolerance are associated with pH changes in the root zone, mineral nutrition, Al uptake and translocation, and Al complexation in the plant (Foy et al., 1978). Soileau et al. (1969) reported that yield reductions in cotton were not related with pH, *per se,* but were inhibited by high levels of soluble Al in the soil, which induced morphological damage to the root system and depressed Ca uptake. Growth reductions occurred when Al concentrations were above 0.2 and 0.02% in roots and tops, respectively. Tissue P increased with decreasing Ca and increasing Al concentrations. The interference of Al on Ca uptake has been hypothesized as a competition for sites of absorption on plant roots (McColl, 1969).

The application of Ca and P to potted soils from the surface and spodic horizons of a Leon fine sand (Aeric Haplaquod) increased growth of oats, millet, and clover (Robertson et al., 1966). Phosphorus was the most important limiting element in both soil horizons. Crop yields and P uptake increased up to the highest rate of P application (88 ppm). Calcium increased plant yields with additions up to 240 ppm Ca and decreased them when the amount of Ca was doubled.

The detrimental effect of Al is generally reduced by the formation of chelates with soil organic matter or plant organic acids. Thawornwong and van Driest, cited by Foy et al. (1978), reported that 0.5 to

2 ppm of ionic Al was lethal to rice seedlings in nutrient solutions but 2 ppm Al in chelate form was not harmful. Humphreys and Truman (1972) studied the effect of Al on the uptake and movement of P in radiata pine seedlings using the culture solution method. They concluded that P uptake was stimulated by increasing Al levels in the solution provided that the P level was adequate; Al uptake was related to Al in the solution and strongly related to the P level in solution; high Al level in the roots did appear to impede P translocation from roots to tops; the amount of Al transported to the tops was negatively affected by the level of P in the roots. For a group of species of eucalypts, McColl (1969) found that foliar P increased as the ratio Ca:Al and P:Al in the soil increased.

Obviously, the level of Al in plant tissue varies with species. Humphreys and Truman (1964) reported that pine species contained Al levels from 475 to 1300 ppm, whereas, eucalypt species growing on the same or similar soils, contained 200 ppm.

Aluminum is not generally regarded as an essential element for plant growth but for some species, low concentration seems to increase growth (Foy et al., 1978). Mullette (1975) stated that in certain plant species, Al has the role of a plant micronutrient. Foy et al. (1978) listed several plant species that have shown positive growth response to Al in nutrient cultures. Tea plants have shown good response to Al concentrations as high as 27 ppm at pH 6.0. Mullette (1975) applied five levels (0, 0.5, 1.0, 10.0 ppm) Al to *Eucalyptus gummifera* and two concentrations of P (1.0, 100.0 ppm) in sand culture and found maximum response at 1.0 ppm Al. Aluminum stimulation to

plant growth was independent of P concentration. Results somewhat similar to those of Mullette, were reported by Qureshi (1978) for *E. saligna* seedlings. He applied six levels of Al (0, 0.5, 1.0, 2.0, 4.0, and 8.0 ppm) as $AlCl_3$ to seedlings planted in pots containing perlite as a growth medium. Levels of Al up to 1.0 ppm stimulated height and diameter growth and increased top weight of the seedlings. The best growth, however, was obtained with the application of 0.5 ppm Al. Aluminum at concentrations of 4 and 8 ppm slightly reduced shoot growth and 8 ppm Al reduced root growth to nearly one half of that of the control. The foliar concentrations of N and P were increased as the level of Al in the growth medium increased but the other nutrients were not significantly affected.

The positive effect of exchangeable Al on growth of *E. alba* trees planted on a Latosol in Brazil (Barros, 1974) was interpreted as an indication of the capability of this species to absorb P from Al-phosphates. Fassbender and Tschinkel (1974) found that Al-phosphates provided the best predicting equation for growth of *Cupressus lusitanica* on volcanic soils in Colombia. A mechanism for explaining the uptake of P from Fe- and Al-phosphates by eucalypt species was proposed by Mullette et al. (1974).

Many of the apparent direct effects of soil acidity on tree growth may result from its indirect effect on soil conditions such as microbial activity and nutrient availability (Pritchett, 1979). Generally the availability of B, Cu, Mn, and Fe is increased as soil acidity is increased.

The importance of acidity as a soil factor affecting site quality of various tree species has been reported by several investigators (Ballard, 1971; Broadfoot, 1969; Mader, 1976; Nemeth and Davey, 1974; Wilde et al., 1964a). Its significance for growth of some species of eucalypts was shown by Anderson and Ladiges (1978), Ladiges and Ashton (1977), and Parsons and Specht (1967), who grew various eucalypt ecotypes in the greenhouse on soils with different pH values. In all cases, ecotypes occurring naturally on acid soils showed severe chlorosis and in many cases developed red and necrotic patches on leaves when grown on more neutral or alkaline conditions. Species adapted to calcareous or alkaline conditions but grown on acidic medium showed some reduction in growth, but not so intense as in the former case.

Soil-Plant Growth and Nutrient Relationships

The concentration of nutrient elements in tree tissue may be correlated with growth and, hence, with soil nutrient supply of the site. The relative quantity of nutrients available in the volume of soil exploited by the roots is assumed to be indicated by the chemical analysis of some tree components, usually the leaves. It should be pointed out that foliar nutrient concentrations are not site parameters and their use as a technique for assessing site quality may not be reliable in many cases (Rennie, 1963). Nevertheless, foliar nutrient concentration is a useful criterion in the determination of the nutritional status of trees.

Poor relations of soil and foliar nutrient concentrations with tree growth may result due to inadequate appreciation of the many

factors which affect these relationships. For example, the results of foliar analysis are strongly dependent upon standardized sampling techniques. A recent review on the causes and factors responsible for variations of nutrients in forest tree foliage was performed by Turner et al. (1978).

Little information is available on foliage sampling procedures for eucalypt species. A specific study for *E. deglupta* was carried out by Lamb (1976) in New Guinea. He found that the factors most strongly affecting foliar nutrient concentrations in this species were leaf age and season. Nitrogen, P, and K concentrations tended to decrease with leaf age, whereas the reverse was observed for Ca, Mg, Fe, and Mn. Seasonal effects were most noticeable with micronutrients, particularly Mn, B, and Fe. Lamb reported, additionally, that a single sampling position is unlikely to be suitable for all elements. He recommended sampling the innermost leaves of the upper crown branches for N, P, and all micronutrients, during the late wet season. Leaves at the outer position should be taken from the upper crown branches for Mg determinations. Leaves from the upper branches are also suitable for K determinations but should be sampled only during the dry season. Calcium was least variable when samples were collected from the lower crown branches.

The relationships between foliar and soil element concentrations and tree growth have been studied for several tree species. Alban (1974) found significant relationships between site index of red pine and surface soil N and P, and between site index and foliar N and P concentrations. A regression equation involving terms for surface soil N, P, and K

accounted for 79% of the variation in site index. Another equation related site index with foliar N, P, and the interaction NK and resulted in a R^2 of 0.67. Positive effect of foliar concentrations of N and P on site index of a spruce bog was also described by Watt and Heinselman (1965) in northern Michigan; K concentrations, however, showed an inverse relationship. This inverse relation was interpreted as a growth dilution effect since the levels of soil K were sufficient on all sites. In California, foliar P concentrations of white fir growing on soil with low available P was significantly related to growth measurements (Isik, 1978). Foliar concentrations of Ca and Mn were directly related to their levels in the soil. Foliar K was positively related with tree growth, regardless of soil chemical properties.

Raupach and Clarke (1978) showed that height of radiata pine increased and diameter decreased with higher foliar N, Cu, and Mn but both increased with higher foliar Zn and Na. In their study, four soil types were included and foliar levels of the various nutrient elements were influenced by soil type. On increasingly swampy phases of Podzols, foliar Cu and Mn decreased but N and Na increased.

McColl (1969) and McColl and Humphreys (1967) reported that the concentrations of the major nutrients in leaves and bark of dominant trees of some eucalypt species followed soil gradients, particularly those of leaf P and bark Ca. The uptake of P by the trees was presumably affected by soil Ca and Mg because of the high correlation of leaf P with these two elements. Bark Ca concentrations were also significantly correlated with soil Mg.

Specific studies have shown that growth of some species of eucalypts can be correlated with levels of foliar nutrient concentrations. For plantations of *E. deglupta* in New Guinea, Lamb (1977) found that height growth and basal area were positively correlated with foliar N and inversely correlated with P, Ca, and Mg. Height growth of two plantations could be predicted by the equation:

$$(\text{Height} = -4.46 + 11.50N - 2.03N^2 - 3.52P)$$

which accounted for 72% of the variation in growth. The volumetric production of five species of eucalypts growing on Latosols in Brazil (Haag et al., 1976) was positively correlated with foliar concentrations of N, P, K, S, and Fe. None of the other elements (Ca, Mg, B, Cu, Mn, Zn) examined in the study was found to affect the yield of wood.

Summary

In summarizing the general soil requirements of eucalypts, it can be said that most species will grow well on moderate to deep soils, with sandy or loamy texture and presenting a good moisture regime. Waterlogged and poorly drained soils are generally unsuitable for eucalypts, although some species, such as *E. camaldulensis*, *E. robusta* and, to a lesser extent, *E. grandis* tolerate periodic flooding. Although many eucalypts can grow on relatively infertile soils, they will respond to more fertile conditions, particularly to N and P rich sites. Most species will not grow on alkaline soils with large amounts of free calcium carbonate or on soils containing high levels of sulfate in the profile. Few species will tolerate soils with high salinity.

In sampling eucalypt leaves for chemical analysis special attention should be paid to leaf age and season. Leaves from the upper crown branches should be sampled during the wet season for all nutrients except K, for which sampling during the dry season provides better results. Leaves for Ca determination should be taken from the lower crown branches.

The success in correlating tree growth with foliar nutrients will depend on sampling procedures, supply of nutrients in the soil, and nutrient interrelationships in both soil and tree. Nitrogen, P, Ca, and Mg are the elements most commonly correlated with eucalypt growth in the few studies that have been carried out.

*Note: Subscripts were used in soil horizon designations to avoid confusion between surface horizon (A_1) and the chemical symbol for aluminum (Al).

MATERIAL AND METHODS

Description of the Study Area

Location and Climate

The study site was located in Glades County in southern Florida, between the geographic coordinates of 26° 50' and 27° 00' north latitude, and 81° 20' and 81° 30' west longitude.

Specific climatic data for the study area are deficient. However, based on climatic data from weather stations located in the nearby towns of La Belle and Moore Haven (Anonymous, 1974), the climate can be classified as subtropical. Summers are long, warm, and relatively humid; winters, although presenting periodic invasions of cool and cold air from the north (Bradley, 1972), are mild. The mean annual temperature registered in both weather stations during the period of 1930 to 1960 was 22.8° C. The coldest month is January with a mean temperature of 17.4° C, while the warmest month is August with a mean temperature of 27.6° C. Occasional frosts occur in the area and temperatures as low as -6.6° C (Anonymous, 1974) have been registered.

The mean annual rainfall is approximately 132.5 cm with 60% of the rain usually falling from June through September. The dry season extends from November through January with monthly averages of 3.5 cm.

Soils and Natural Vegetation

The geologic formations in Glades County (Klein et al., 1964) range from very deep (approximately 90 m) dolomite, dolomitic limestone, and chalky limestone of Eocene age to superficial organic soils of Recent age. The soils of the study site are of the Pleistocene Epoch, originated from marine deposits (Klein et al., 1964) and are mainly composed of quartz sands. According to the American soil taxonomic system (Soil Survey Staff, 1975), the soils of the area are members of the sandy, siliceous, hyperthermic family of the great group Haplaquods. Four soil series were identified in the study site; Immokalee which belongs to the Arenic subgroup covers about 61% of the area, Myakka and Smyrna of the Aeric subgroup, are equally represented and finally, a very few spots, comprising about 2% of the area, were classified in the Ona series, which is of the Typic subgroup of Haplaquods. These soils are very similar in most characteristics; the depth to the spodic horizon (B_2h) and the presence or absence of an A_2 horizon being the differentiating characteristics. The absence of the A_2 horizon differentiates the Ona series from the other three, while the depth to the B_2h horizon serves to separate Immokalee, Myakka, and Smyrna series from each other. In the Immokalee series the depth to the B_2h horizon is 75 cm or deeper, in the Myakka series it is found between 50 and 75 cm, and in the Smyrna series the B_2h horizon is shallower than 50 cm. The generally poor drainage conditions are common characteristics of those soils.

The natural vegetation supported by these soils was very similar and consisted mainly of saw palmetto [*Serenoa repens* (Bartram) Small], scattered wire grass (*Aristida stricta* Michaux), wax myrtle (*Myrica cerifera* L.), runner oak (*Quercus pumila* Walter), and gallberry (*Ilex glabra* (L.) Gray). Slash (*Pinus elliottii* var. *densa*) and longleaf (*P. palustris*) pines are also members of the native vegetation on these types of soils but they have not regenerated after being cut. The past uses of the area have included forest and rangeland.

Characteristics of the Stand

The study was conducted in a relatively well stocked 4-year-old plantation of *Eucalyptus grandis,* planted in June 1973, in an initial spacing which provided about 1,020 seedlings per hectare. The plantation consisted of two adjacent stands, herein called NW and SW stands of 24 ha each. Site preparation consisted of webbing, chopping, and bedding in the NW stand and double chopping and bedding in the SW stand. Half of the NW stand received 2 tons of ground rock phosphate per hectare, while the other half and the SW stand received 1 ton per hectare. Containerized seedlings were machine planted in both stands.

Field Procedures

Sampling Design and Plot Establishment

After preliminarily mapping the study area by soil series, heights and diameters of 30 trees in each series were measured in order to estimate the number of plots needed to provide a precision of at least 5%. Although it was calculated that 24 plots would provide that

precision, 50 plots were proportionally distributed in the study area, based on the area size of each soil series. Therefore, 31 plots were randomly allocated in the Immokalee series, 7 on the Myakka, 11 on the Smyrna, and 1 in the Ona series.

The plots were rectangular in shape with area of 120 m^2 and included 10 to 12 measurable trees. In allocating each plot the soil was probed in transects to assure that the difference in depth to the B_2h horizon between 2 probing points was no greater than 30 cm. Each corner of all plots was marked with aluminum stakes and, additionally, a piece of galvanized pipe was driven into the soil at the NW corner of each plot until its height was about 0.5 m. A metalic label with the plot number was attached.

Stand Measurements and Sampling Procedures

Stand measurements included total height and diameter at breast height (DBH) of all living trees whose diameters were larger than 2.0 cm.

Leaf samples were collected from all measured trees from the upper third on the east side of the crown, using a pole-clipper (or a rifle for trees whose crown could not be reached with the pole-clipper). Only completely mature leaves were sampled. The samples were subsequently dried to constant weight at 67° C.

Soil samples were collected from the bedded rows to a depth of approximately 30 cm and from major soil horizons to 2.0 m depth using a 10-cm diameter soil auger. Color of moist samples was determined in the field from Munsell color charts. Thickness of the major horizons was measured during the soil sampling process.

Hardness of the B_2h horizon was determined with a Proctor penetrometer at 4 different occasions, i.e., August and December 1977, and March and June 1978, in order to obtain a range in soil moisture contents.

Depth to water table was also measured at the same time, and additionally in December 1978 and March, May, and June 1979.

Root System Study

Root system distribution by soil horizons and biomass were studied in the field by excavating 6 trees growing in sites selected on the basis of depth and thickness of the spodic horizon. Three classes of depth (<50, 50 to 75, and >75 cm) and three classes of thickness (<20, 20 to 40, and >40 cm) of spodic horizon were represented (Table 1).

Table 1. Depth to and thickness of the B_2h horizon of the plots selected for studying root systems.

Plot	Depth to B_2h	Thickness of B_2h
	---------- cm ----------	
1	52	22
2	130	45
3	105	52
4	80	18
5	31	15
6	85	22

The size of the area to be excavated around each tree was based on the mean area (9.80 m^2) per tree at planting time. At each site,

the diameters of a few well-stocked trees were measured and the tree of approximate mean diameter and height was selected for excavation. A plot of 4.10 x 2.40 m was marked and it was assumed that the weight of roots growing in the plot would be representative of the root biomass for similar conditions. The results obtained in that plot were used to extrapolate root biomass to a hectare basis. To estimate root distribution by horizons, roots were collected from two subplots 25 cm wide, both having the tree as the starting point, but one going along and the other going across the bed until reaching the boundaries of the plot. The samples collected from those subplots were spread on a wire screen and the soil removed by water under low pressure from a fire hose. The roots were weighed, bagged, and taken to the laboratory for classification and dry weight determination. After collecting roots from the subplots, one-fourth of the plot was shoveled onto the screen using a tractor-mounted backhoe. The soil was washed out and the roots were weighed and sampled for size classification and dry weight determination.

The stump was completely removed, washed, and weighed. The roots were classified into fine (<2.5 mm) and large (>2.5 mm) roots.

The above-ground part of the tree was measured for length, diameter (DBH), and total weight.

Greenhouse Experiment

To study the effect of Al in the B_2h horizon as a chemical barrier to root growth, a greenhouse trial was carried out by applying increasing levels of Al to spodic horizon material. Soils were collected

from the A_1 and B_2h horizons in the NW stand close to the plot whose Al level was previously determined as low. The soil was air-dried and sieved to pass a 20-mesh screen. Samples were taken from each horizon for laboratory analyses.

Aluminum chloride was mixed with six portions of 10 kg of the B_2h soil to provide respectively 0, 1, 5, 25, 125, and 625 ppm of Al above the ambient level. Each portion was then equally divided to form 4 replications and placed in the bottom of 5.0 kg-capacity plastic pots. The upper half of the pots was filled with 2.5 kg of A_1 soil, which was previously mixed with a NPK mixture (4-8-4) in a dosage of 2 g of fertilizer per kg of soil. The N, P, and K sources were reagent grade NH_4NO_3, $CaHPO_4$, and KCl, respectively. The holes in the lower part of the pots were sealed with adhesive tape to prevent leaching. Four graded (3 to 4 cm) seedlings of *E. grandis* were transplanted into each pot. Three times during the 5 month-experimental period, 1 g of the NPK mixture was dissolved in water and applied to each pot. A micronutrient solution was applied to provide 0.5 ppm of B, 5 ppm of Cu, 25 ppm of Fe, 125 ppm of Mn, 0.05 ppm of Mo, and 5 ppm of Zn. Frequent application of insecticide was necessary to control spider mite attack.

At the end of the experiment, total height and fresh and dry weight of shoot and root were assessed. The weight of roots growing in the A_1 soil was assessed separately from that corresponding to roots in the B_2h soil.

Soil samples were also collected separately by soil horizon for laboratory analysis. The shoots and roots were dried to constant weight at 67° C, weighed, and ground to pass a 20-mesh sieve.

Laboratory Analysis

Soil Analysis

Soil samples were air-dried, passed through 2-mm sieves, extracted with double-acid reagent (4:1 reagent:soil ratio), and the filtrate analyzed for P, Ca, Mg, Na, K, Al, and Fe. Organic carbon and pH determinations were also performed. Samples of the A_1 and B_2h horizons were, additionally, analyzed for total N, total P, and cation exchange capacity (CEC). Determinations of pH and N KCl-extractable Al were also performed on moist samples of these two horizons.

Moisture content of the samples was determined so that correction could be made for weight of water.

Soil pH was determined with a glass electrode in a 1:2 soil-water and 1:1 soil-N KCl suspensions. Soil organic carbon was determined by a modified Walkley-Black wet digestion method (Jackson, 1958); total N by the macro-Kjeldahl procedure (Bremner, 1965); and CEC by NH_4 saturation (Chapman, 1965) using N NH_4 OAc acidified with HOAc to pH 4.20 which was the mean pH of the samples. For total P, 100-mesh soil samples were fused with sodium carbonate (Kanehiro and Sherman, 1965) and P determined in the 4N HCl digest by the ascorbic acid method (Watanabe and Olsen, 1965). Determination of K and Na was performed by flame emission spectroscopy and Ca, Mg, Al, and Fe by atomic absorption spectrophotometry.

Moisture retention at 0.1 and 15 bars was determined for samples of the A_1, A_2, and B_2h horizons by the use of a pressure-membrane apparatus (Richards, 1965). Particle size distribution in samples of

A_1 and B_{2h} horizons was determined by the hydrometer method (Bouyoucos, 1951).

The soil samples from the greenhouse experiment were extracted with double-acid reagent and analyzed for Ca, Mg, Na, K, Al, and P. Soil pH was determined on moist samples in water and N KCl suspensions, and on dry sample in water suspensions. Aluminum content was also determined in N KCl extracts of moist samples.

Plant Tissue Analysis

Plant tissue was dried to constant weight at 67° C and ground to pass a 20-mesh sieve. Nitrogen concentrations were determined by the macro-Kjeldahl method (Bremner, 1965). Analyses for other nutrients were performed by ashing 0.5 to 1.0 g of tissue in a muffle furnace at 500° C for 5 hours; the ash was taken up with 0.1 N HCl, filtered, and the volume completed to 50 ml. Phosphorus was determined by the ascorbic acid method (Watanabe and Olsen, 1965), K and Na were determined by flame emission, and Ca, Mg, Al, Mn, and Cu by atomic absorption spectrophotometry.

Statistical Treatment of Data

Over 150 variables including results of field soil measurements, soil physical and chemical properties analyzed in the laboratory, and tissue analyses were analyzed by regression procedures. Many variables were derived from mathematical transformations, such as interactions, ratios, and quadratic terms, and by expressing concentrations on the kg/ha basis. The variables significantly correlated with tree growth and included in the selected regression equations are coded in Table 2.

Tree volume was calculated using the formula*

$$V = d^2(0.001818\ H + 0.01636)$$

where V = volume in cubic feet, d = DBH in inches, and H = total height in feet, and transformed to volume in m^3/ha taking into consideration the number of trees per plot.

The stepwise multiple regression and correlation procedures, as available in the SAS program (Barr et al., 1976), were used to relate measures of growth (dominant and mean tree heights and volumes/ha) with soil factors and foliar nutrients and to relate foliar nutrients with soil factors. In selecting the regression equations the criteria established were that both the equation and the variables in the equation had to be significant at least at the 5% level. The coefficient of determination (R^2) was used as a measure of usefulness of the regression equations and the standard error of the estimate (SEE) calculated to indicate the precision of estimation of each selected model.

The following additional statistical variables, as suggested by Fowler and Bigelow (1979), were used for evaluating some of the selected regression equations:

$$R^2_{Adj.} = 1 - (1 - R^2)\ \frac{n-1}{n-p-1},$$

$$1 - \frac{MSE}{MS\ Total},$$

$$D(R^2_0) = E(R^2)/\mu_R 2{=}0) = p/(n-1),$$

and

* Geary, T. F., personal communication

$$E'(R^2) = (\mu_R2 + p(1-\mu_R2)/n-1) - 2(n-1-p)\mu_R{}^2(1-\mu_R2)/(n^2-1)$$

where

$R^2{}_{Adj.}$ = an adjusted R^2 for n observations and p dependent variables in the equation; MSE and MS Total = the mean squares for the error term and total sum of squares; $E(R_0^2)$ and $E'(R^2)$ = the expected R^2 for populations with $\mu_R2 = 0$ and $\mu_R2 > 0$, respectively.

Recognizing that the variables in the equations calculated by stepwise regression procedures may present a high degree of interdependence, ridge regression procedures[1] were applied to a few of the selected equations in order to evaluate the magnitude of the dependence among these variables.

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[1]The author acknowledges Mr. M. Conlon for providing the computer program for ridge regressions.

Table 2. Dependent and independent variables and codes included in the selected regression equations and correlation studies.

Variable	Unit	Code
Mean height of the dominant trees	m	HD
Mean height of all measured trees	m	HM
Mean diameter of all measured trees	cm	DM
Volume of wood	m^3/ha	VOL
Concentration of tissue N	%	N
Concentration of tissue P	%	P
Concentration of tissue K	%	K
Concentration of tissue Ca	%	Ca
Concentration of tissue Mg	%	Mg
Concentration of tissue Na	%	Na
Concentration of tissue Mn	ppm	Mn
Concentration of tissue Cu	ppm	Cu
Concentration of tissue Al	ppm	Al
Thickness of the A_1 horizon	cm	A1TH
Thickness of the A_2 horizon	cm	A2TH
Thickness of the B_2h horizon	cm	BTH
Hardness of the B_2h horizon	kg/cm^2	STR
Depth of the water table in the fall	cm	DWTF
Depth of the water table in the spring	cm	DWTSPR
Moisture retention at 0.1 bar of A_2 horizon	%	A2FC
Moisture retention at 0.1 bar of B_2h horizon	%	BFC
Moisture retention at 15 bars of the B_2h horizon	%	BWP
Water availability of B_2h horizon	%	BWA
Coarse sand in the A_1 horizon	%	CSNA
Silt in the A_1 horizon	%	SIA
Clay in the A_1 horizon	%	CLA
Silt plus clay in the A_1 horizon	%	SICLA
Sand in the B_2h horizon	%	SNB
Very coarse sand in the B_2h horizon	%	VCSNB
Coarse sand in the B_2h horizon	%	CSNB

Table 2. Continued

Variable	Unit	Code
Medium sand in the B_2h horizon	%	MSNB
Very fine sand in the B_2h horizon	%	VFSNB
Silt in the B_2h horizon	%	SIB
Clay in the B_2h horizon	%	CLB
Silt plus clay in the B_2h horizon	%	SICLB
Fine fractions (SICLB + FSNB + VFSNB) in the B_2h horizon	%	FF
Depth to the B_2h horizon	cm	D
Ratio between D and BTH	ratio	D/BTH
Ratio between D and STR	cm^3/kg	D/STR
pH of the bedded soil		SPH
pH of the A_1 horizon		A_1PH
pH of the A_2 horizon		A_2PH
pH of the B_2h horizon		BPH
Average of SPH and A_1PH		MPH
Calcium in the bedded soil	ppm	SCA
Calcium in the A_1 horizon	kg/ha	CAKG
Calcium in the A_2 horizon	ppm	A_2CA
Calcium in the B_2h horizon	ppm	BCA
Sum of Ca in the bedded and A_1 horizon soil samples	ppm	SACA
Magnesium in the A_1 horizon	ppm	A_1MG
Magnesium in the A_2 horizon	ppm	A_2MG
Magnesium in the B_2h horizon	ppm	BMG
Sum of Mg in the bedded and A_1 horizon soil samples	ppm	SAMG
Potassium in the bedded soil	ppm	SK
Potassium in the A_2 horizon	ppm	A_2K
Sum of K in the bedded and A_1 horizon soil samples	ppm	SAK
Sodium in the A_1 horizon	ppm	ANA
Sodium in the B_2h horizon	ppm	BNA
Aluminum (D.A. extracted) in the bedded soil	ppm	SAL
Aluminum ($\underline{N}$ KCl extracted) in the A_1 horizon	ppm	AKAL
Aluminum (D. A. extracted) in the A_2 horizon	ppm	A_2AL
Aluminum (D. A. extracted) in the B_2 horizon	ppm	BAL

Table 2. Continued

Variable	Unit	Code
Aluminum ($\underline{N}$ KCl extracted) in the B_2h horizon	ppm	BKAL
Iron in the A_1 horizon	ppm	AFE
Iron in the B_2h horizon	ppm	BFE
Nitrogen in the A_1 horizon	ppm	A1N
Nitrogen in the B_2h horizon	ppm	BN
Phosphorus in the bedded soil	ppm	SP
Phosphorus in the A_1 horizon	ppm	A1P
	kg/ha	PKG
Phosphorus in the A_2 horizon	ppm	A2P
Phosphorus in the B_2h horizon	ppm	BP
Sum of P in the bedded and A_1 horizon soil samples	ppm	SAP
Ratio A1N/A1P	ratio	ANPR
Organic carbon (OC) in the bedded soil	%	SOC
Organic carbon in the A_1 horizon	%	A1OC
	kg/ha	OCKG
Organic carbon in the A_2 horizon	%	A2OC
Organic carbon in the B_2h horizon	%	BOC
Sum of OC in the bedded and A_1 horizon soil samples	%	SAOC
Cation exchange capacity (CEC) in the B_2h horizon	meq/100g	CECB
Rates of ground rock phosphate (GRP) application	kg/ha	GRP
Product of D and BKAL	cm x ppm	DBKAL

RESULTS AND DISCUSSION

Relationships Between Soil Properties and Eucalypt Growth

The results of the chemical and physical analyses (Table A1) of soils of the study area confirm the generally low fertility, high acidity, and sandy character of Spodosols in Florida (Calhoun and Carlisle, 1974). The nutrients were mostly concentrated in the bed and in the A_1 and spodic (B_2h) horizons. Comparatively low nutrient concentrations were found in the leached A_2 horizon, except for Ca which was found in similar amounts to that in the B_2h horizon. Calhoun and Carlisle (1974) reported that the Ca contents in the $B_{21}h$ horizon of Florida Spodosols were generally about four times greater than in the A_2 horizon. In the present study, the relatively high Ca content in the A_2 horizon is probably a consequence of Ca eluviation from the A_1 horizon, to which high amounts of ground rock phosphate were applied.

Soil pH, extractable bases, and CEC were comparable to the lowest values reported by Calhoun and Carlisle (1974) and indicated the poor conditions for plant growth of the soils of the study area. The content of organic matter was slightly lower than the mean value reported by those investigators, while the CEC and moisture retention capacity of both the A_1 and B_2h horizons were well below their values. In the present study, the amount of fine textured material was smaller than that reported by Calhoun and Carlisle and a lower moisture retention capacity was expected.

The results in Table A1 show the similarity among the three soil series included in this study for most soil properties. However, the standard error indicated that considerable variation existed among individual values of some soil properties, both within and among soil series. These variations constituted the basis for the hypothesis of the present study and were expected to explain some of the variations observed in the growth of *E. grandis* in the study area.

The annual rate of height growth of the *E. grandis* used in this study (Table A3) was lower than that (3.0 m) considered normal for this species (Anonymous, 1976) and well below the rates that have been obtained in other countries where it has been planted as an exotic species. The volume per hectare was particularly low.

Tree growth was significantly different among soil series. Both tree height and volume in the Immokalee and Myakka series were significantly greater than in the Smyrna series. However, as indicated by the standard error, all growth parameters, with the exception of mean height, tended to present lesser variation in the Myakka and Smyrna than in the Immokalee series. Possible reasons for those differences are discussed in later sections.

Single Soil Properties Affecting Tree Growth

The effects of single soil properties on tree growth were studied using matrix of correlation, graphs, and simple linear regressions. However, it should be pointed out that these approaches provide no information on the independent contribution of a given soil feature to the variation in tree growth. In other words, the relationship between the soil variable and tree growth may, indeed, reflect an

indirect effect of other variables. In the present study, attempts were made to explain each case based on the biological significance of the relationship.

The relationships between soil properties and tree growth were statistically analyzed, first considering the data for the whole area regardless of soil type and then by soil series. This approach permitted one to distinguish three patterns in the soil-tree growth relationship. First, if a soil property was closely related to tree growth in all three soil series it was, consequently, very important in explaining growth variation in the whole study area. The second pattern occurred when a soil property was significantly correlated with tree growth in one or two of the soil series. In this case, the effectiveness of this property in explaining growth variation in the whole area depended on the degree of its correlation with the growth measurement, and/or on the number of observations to which the relationship was significant. Finally, the third pattern appeared when a soil property, not being significantly correlated with tree growth in any of the soil series, showed a definite and significant relationship with growth as the data were analyzed for the overall area. Because of those patterns, the results are presented and discussed, first considering the whole study area and then by soil series.

Tree growth as related to soil chemical properties

Those soil chemical properties significantly correlated with eucalypt growth in the study area and in each soil series are shown in Table 3. Surface soil pH (MPH and AlPH) was the soil property that presented the closest correlation with tree growth. The decrease in

Table 3. Correlation coefficients between tree growth parameters and selected soil chemical properties.

Soil chemical property	Soil series															
	Immokalee (n = 32)				Myakka (n = 7)				Smyrna (n = 11)				Study area (n = 50)			
	HD(†)	HM	VOL	OM	HO	HM	VOL	OM	HO	HM	VOL	OM	HO	HM	VOL	OM
MPH(†)	-0.48	-0.44	-0.49	(††)		-0.94	-0.96	-0.94					-0.55	-0.55	-0.51	-0.47
SOC	0.39		0.48						0.71	0.72			0.40	0.28	0.32	
SP				0.46												
SAK	-0.62	-0.49		-0.58						0.64		0.65	-0.30			
SCA				0.46								0.66				0.30
SACA						0.92	0.87	0.82								
SMG										0.64						
SAMG	-0.45	-0.41			0.86											
SAL	0.65	0.61	0.54	0.59									0.30			
A_1PH									-0.87	-0.64						
A_1P									-0.71							
AFE	0.47	0.36	0.44						-0.72	-0.72		-0.70				
A_2PH							-0.82	-0.82								
A_2OC					0.89											
A_2P					0.85											
A_2K	-0.44												-0.32	-0.35	-0.41	
A_2CA					0.84			0.80								
A_2MG					0.83											
A_2AL					0.77											
BPH						-0.87	-0.91	-0.92		-0.72	-0.62	-0.61	-0.35	-0.48	-0.49	-0.45
BOC										0.78	0.64		0.35	0.41		0.33
BN	0.40								0.60	0.68						
BP	0.36									0.76		0.75	0.35	0.32	0.38	
BCA											0.62					
BMG										0.70	0.67	0.63		0.33		0.34
BKAL	0.40												0.40	0.37	0.35	0.30
BNA						0.90	0.93	0.87					0.34	0.39	0.38	0.38
BFE														-0.32	-0.30	
CECB	0.40									0.77	0.81	0.63	0.44	0.44	0.33	0.44

(†) Codes are defined in Table 2. (††) Only significant values (<5% level) are shown.

soil pH was associated with significant increases in tree height and diameter and volume per hectare. The soils in the study area were very acid (Table A1) with pH values ranging from 3.55 to 4.05 and tree growth was expected to show a positive relationship with soil pH. Negative relationships between tree productivity and soil pH have been reported in other studies (Ballard, 1971; DeMent and Stone, 1968). Soil pH, by itself, is not a productivity factor and its relation to tree growth is generally indirect; i.e., reflecting its effect on other soil factors, such as nutrient availability. DeMent and Stone (1968) stated that the inverse relationship between soil pH and site index of red pine was spurious and caused by a few plots with poor drainage. Ballard (1971) concluded the negative relationship observed between soil pH and productivity of radiata pine in New Zealand reflected an indirect effect of pH on soil extractable P. In the present study, the effect on tree growth is also believed to be indirect through its relations with such soil factors as soil organic carbon and P, or due to its effect on the dissolution rates of GRP (ground rock phosphate). The decrease in pH was associated with higher content of organic carbon ($r = -0.37$) in the surface soil and P($r = -0.49$) in the B_2h horizon. Organic matter is a very important nutrient reservoir and, hence, a source of nutrients in sandy Florida soils. Tree growth was generally better on soils with higher organic matter contents (Table 3). Because soil organic matter was positively correlated with soil contents of Ca, Mg, K, and N, its increase in the soil represented a better nutrient regime for eucalypt growth.

The negative relationship between soil pH and P content of the B_2h horizon is probably a consequence of higher dissolution rate of ground rock phosphate (GRP) at lower pH values. This increased dissolution of GRP at lower pH values would result in higher contents of P and Ca and consequently better tree growth.

Growth of young pines has also been significantly increased on flatwood and savanna soils by the application of P fertilizers (Pritchett and Gooding, 1975; Pritchett and Smith, 1975). Radiata pine also failed to grow satisfactorily on the extremely acid Spodosols in Australia unless P was added through fertilization (Raupach, 1967a). The flatwood soils in Florida, besides being P deficient generally have a low capacity to retain P in the soil surface due to their low extractable (less than 40 ppm) Al and Fe (Pritchett and Gooding, 1975) and slowly soluble phosphates (GRP) are preferred sources (Ballard and Pritchett, 1974). In the present study, it appears that a large portion of the P released from the GRP and not taken up by plants was translocated to the B_2h horizon where the content of Al and Fe is much higher than that in the surface soil layer (Table A1). In spite of the low P retention capacity in the A_1 horizon, it is apparent that some P fixation took place in this layer as deduced from the significant correlation between the content of total P and the contents of double acid extracted Al ($r = 0.41$) and Fe ($r = 0.28$).

The content of organic carbon in one or more horizons was positively correlated with tree growth in one or more soil series (Table 3). The relationship between the content of organic carbon in the bedded soil and the mean height of the dominant trees is

illustrated in Figure 1. The importance of the organic matter as a source of nutrients for tree growth has been reported by several investigators (Mader, 1976; Mader and Owen, 1961; Wilde et al., 1964a, b) and its relevance as a source of such elements as Mg, K, and N in the study area was already pointed out. In the sandy Florida soils, organic matter is also the main source of cation-exchange sites (Fiskell, 1970) and, thus, fundamental in regulating the exchangeable cation regime in the soil. The CEC of the soils of the study area was highly correlated ($r = 0.81$) with organic carbon content.

Another possible role of organic matter in these soils is the complexation of part of the exchangeable Al which otherwise could cause plant toxicity. This has particular significance in the B_2h horizon where the Al content is high. Organic compounds extracted from the B_2h horizon form very stable complexes with Al (Schnitzer, 1969). Moisture retention capacity in soils with coarse texture is highly dependent on soil organic matter. The correlation between soil organic carbon and variables indicative of moisture retention was very high ($r = 0.67$) in this study. Improved moisture retention may have a great importance in eucalypt growth in the study area particularly during drier periods when the water table lowers in the profile. During these occasions water deficiency is likely to occur mainly in the surface horizon.

The relations of organic matter with soil nutrients, moisture retention, and eucalypt growth in the present study have a profound practical significance. It is clear from these results that reasonable yields on these soils will depend to a great extent on the maintenance of adequate levels of organic matter. It has been shown that

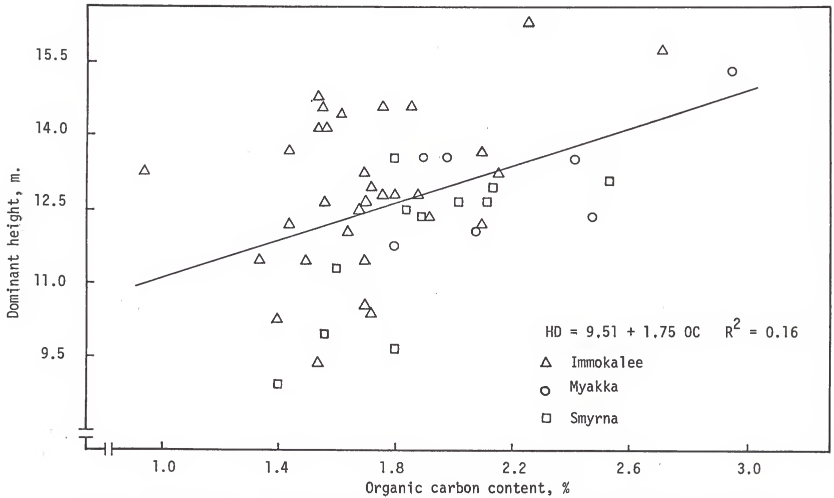

Figure 1. Relationship between organic carbon content in the bedded soil and dominant height of *E. grandis* in South Florida.

intensive practices of site preparation may remove a considerable part of the organic matter from the site on some Florida Spodosols (Burger, 1979). While the addition of chemical fertilizers may replenish nutrients to the soil for a certain period of time, this practice may be uneconomical and does not provide for the physical and "buffer" effects of soil organic matter. Therefore, conservative management practices seem likely to be necessary on these soils.

Tree growth was significantly affected by soil Ca, Mg, and K in this study (Table 3). The increase in soil Ca was associated with better diameter growth, whereas the relationship between soil Mg or K with growth, whether a positive or negative relationship, depended on soil series. Soil Ca content in most samples was between 55 and 130 ppm with a few values between 150 and 200 ppm. These values are lower than the mean value reported by Calhoun and Carlisle (1974) for a group of Spodosols and generally lower than the Ca content for other soils belonging to the same series in Florida (Carlisle et al., 1978). According to Pritchett and Gooding (1975), soil Ca is seldom a limiting factor to pine growth in the flatwoods. However, the level of fertility required by eucalypts for good growth is higher than that for most pines (Anonymous, 1976).

The critical level of soil nutrients for adequate eucalypt growth is yet to be established. In Brazil, mean height of *E. alba* was positively affected by Ca increases in soil in which the levels were generally higher than those reported herein. The average of 105 ppm was, nonetheless, higher than that reported by Haag et al. (1976) and for which no significant relationship with volume growth of several

species of eucalypts was obtained. In the present study, higher soil Ca concentrations were consistently associated with better tree diameter growth but only in the Myakka series were height and volume significantly better on soils with higher Ca contents. In spite of the highly significant correlation, it must be remembered that the Myakka series is represented by only seven plots. Therefore, it seems reasonable to say that in general, soil Ca is not limiting eucalypt height growth in the study area. In fact, this was expected because the high amounts (1 ton and 2 tons/ha) of GRP applied to the area should provide much of the Ca needed for tree growth.

The relationships between surface soil K or Mg and tree growth were negative in the Immokalee series (deep spodic), whereas they were positive in the Myakka and Smyrna series (Table 3). Potassium concentrations in the surface soil were very low, ranging from about 4.4 to 8.8 ppm as shown in Figure 2. This is even lower than the critical level of soil K for slash pine in the coastal plain of about 10 ppm as reported by Pritchett and Gooding (1975). Eucalypt responses to K applied alone have been rare (Barros, 1977; Schutz, 1976). Mello (1968) concluded that the application of fertilizers to *E. saligna* grown on a soil with 16 ppm of exchangeable K was justified only because of a significant NK interaction.

In the present study, the level of soil K was low and any increase of this element seems unlikely a cause of growth reduction. Hence, the negative relationship on the Immokalee series was probably an indirect one. Examining the relationship of K with other soil factors in the Immokalee series, a highly significant negative correlation

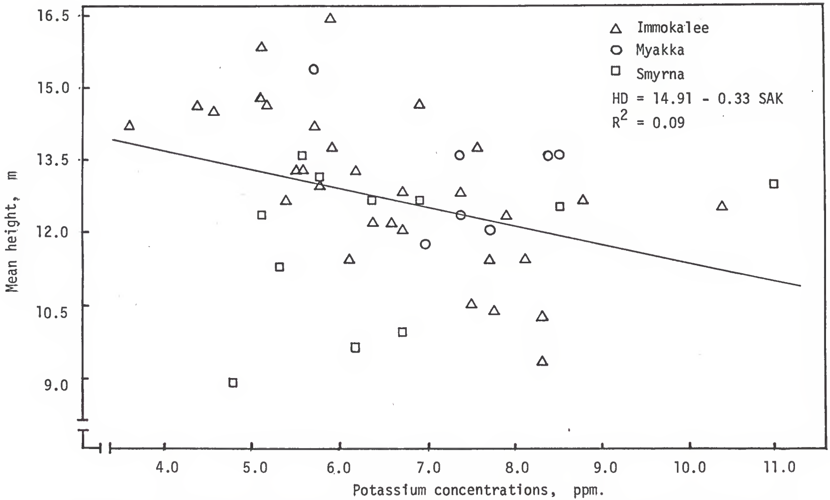

Figure 2. Relationship between K concentrations in the surface soil and mean height of *E. grandis* in South Florida.

(r = -0.67) was found between soil K and rates of GRP. When the data were stratified by GRP application, the relationship of soil K and tree growth was not significant. This indicates that the negative effect of soil K on tree growth in the Immokalee series was indirect. When the same analysis was performed on data for the whole area, there was a positive effect of increasing level of surface soil K on height growth. Therefore, it is likely that the additions of K fertilizers to the overall area would result in increased eucalypt growth.

The negative relationship between surface soil K and rates of GRP has, nonetheless, a practical significance. It means that as the rate of GRP was doubled from 1 to 2 tons/ha there was a reduction in the content of K in the surface soil, probably due to leaching. As pointed out before, the CEC of the soils of the study area was low and highly dependent on organic matter. The bonding strength of exchangeable sites of organic matter for cations such as K is not great (Tisdale and Nelson, 1976). The higher rate of GRP probably released a relatively high amount of Ca which could have displaced K from the exchange sites. In fact, the mean content of surface soil K in the plots receiving 2 tons of GRP was 2.8 ppm, whereas in those plots receiving 1 ton, it was 3.8 ppm. Soils receiving 2 tons/ha of GRP had 6.6 ppm of K in the B_2h horizon as compared to 2.0 ppm in plots receiving 1 ton GRP/ha. While these differences were not statistically tested, they would likely be significant. Specific studies are needed to provide a better understanding of the soil K-GRP relationship. Due to the apparent soil K deficiency, studies involving K fertilizer application to eucalypt plantation in the area are recommended.

The relationship between soil Mg and tree growth followed much the same pattern as that of soil K-tree growth. Again the significant negative effect of surface soil Mg on tree growth in the Immokalee series disappeared when corrected for the effect of GRP rates. Hence, the effect of soil Mg on tree growth on this soil series is indirect through its relationship with GRP. The levels of soil Mg were very low, ranging from 6 to 35 ppm in the surface horizon with a mean of 12.8 ppm. These values are even lower than the minimum level of soil exchangeable Mg for acceptable growth of jack pine which was suggested to be 36 ppm (Wilde et al., 1964a).

In spite of the low soil Mg level in these flatwood soils, the element is not usually limiting to slash pine growth (Pritchett and Gooding, 1975) and growth responses to Mg fertilizer application have shown little promise (Pritchett and Smith, 1975). Haag et al. (1961) reported that the uptake of Mg by 2-year-old trees of slash pine and *E. grandis* produced a ratio of 1:4.47. Although it is clear that eucalypts have a relatively higher Mg requirement as compared to slash pine, the feasibility of Mg fertilizer application to the area is economically questionable.

Tree height and volume were significantly related to P concentrations in the B_2h horizon. As shown in Figure 3, P concentrations in this horizon were, in many plots, below 2.0 ppm which is considered the critical level for slash pine in the coastal plain of the southeastern United States. This positive correlation between P concentrations and tree growth seems, however, to reflect the effects of GRP application. The spodic horizons of plots which received 2.0 tons

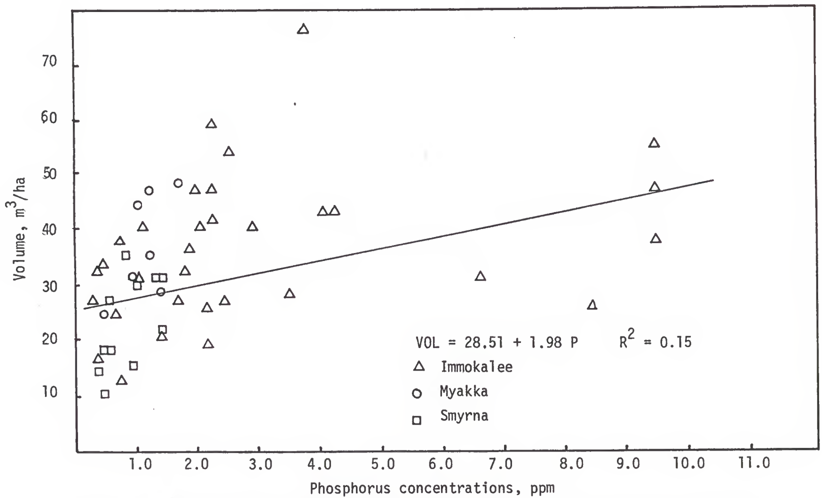

Figure 3. Relationship between P concentrations in the spodic horizon and volume of *E. grandis* in South Florida.

GRP/ha contained an average P concentration of 3.8 ppm, whereas in plots receiving 1.0 ton GRP/ha, the spodic horizons contained an average of 1.5 ppm P. This suggests that P leaching took place when the higher rate of GRP was used because the low P-fixing capacity of the surface soil and limited plant capacity to uptake all the released P. Thus, a large portion of the translocated P probably becomes inaccessible to the trees due to the formation of insoluble Fe- and Al-P compounds in the spodic horizon and the lack of effective rooting in this horizon.

Surface soil (bed plus A_1 horizon) P concentrations averaged 10.6 ppm when the whole study area was considered and no positive effect on tree growth occurred with increasing P concentrations in this layer. Therefore, it appears that the area has adequate P supply for eucalypt growth. This was expected as a result of the application of 1 or 2 tons of GRP to all plots. The reasons for the negative relationship between soil P in the A_1 horizon and dominant height of the trees in the Smyrna series (Table 3) are not apparent.

The relationship between total N in the spodic horizon and tree height was significant in the Immokalee and Smyrna soils (Table 3). This relationship, however, appears to be an indirect one because no significant correlation was observed between total N in the A_1 horizon and tree growth. The concentration of N in the A_1 horizon ranged from 0.02 to 0.09% with an average of 0.05%, whereas the average concentration in the spodic horizon was 0.04% (Table A1). The minimum soil N concentration for good eucalypt growth has not been established. However, it appears that the soils of the study area are N deficient

because significant growth responses to N fertilizer application to *E. grandis* plantations in southern Florida have been obtained. Barros and Pritchett (1978) found that applications of 200 kg/ha of NH_4NO_3 to 3-year-old *E. grandis* plantation resulted in height and diameter increments that were 69% and 76% higher than the unfertilized control. This indicated that N was a growth-limiting factor in the study area and that N fertilizers applied to eucalypt plantations on these soils should result in growth increases.

The type of N fertilizer and time of application on these soils deserve special attention. *Eucalyptus grandis* is native to ecosystems in which the soils are more fertile and better drained than those in southern Florida and nitrification is likely to occur under those conditions. Therefore, it is quite probable that this species meets at least part of its N needs in the NO_3 form. Little nitrification takes place under the very acid conditions existing in the Spodosols of southern Florida and, consequently, NH_4 is probably the only available N for plant growth. Furthermore, the high acidity and fluctuating water table favor the process of denitrification, while the sandy texture favors NO_3 leaching to deeper portions of the soil profile. Hence, applications of NO_3-N should be at rates designed to match plant uptake and it should be done when the water table is at some distance below the soil surface. The sandy texture and low CEC of the surface soil indicate that slow-release N fertilizer may produce better results than soluble forms.

Figure 4 shows that the increase in the growth with the decrease in pH of the B_2h horizon is an indirect effect due to the relationship

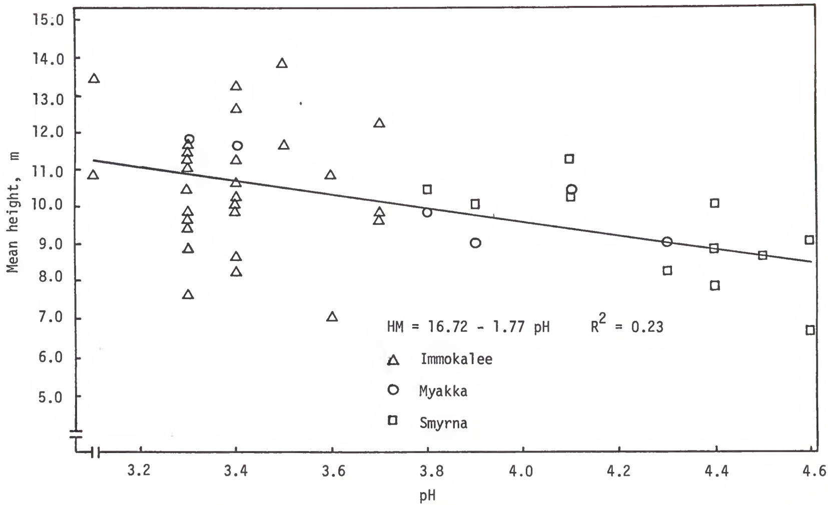

Figure 4. Relationship between pH of the spodic horizon and mean height of *E. grandis* in South Florida.

between pH and soil series, i.e., depth to the spodic horizon. The pH values were higher in the spodic horizon of Myakka and Smyrna than those in Immokalee series. The positive relationship between tree growth and exchangeable Al in the B_2h horizon was also due to the effect of the B_2h horizon depth. Soils with deep B_2h horizons contained larger amounts of exchangeable Al than soils with shallow B_2h horizons (Table A1).

Tree growth was better on soils with B_2h horizons having high CEC than on those where the CEC was low. The effect of CEC on growth is probably indirect because of its high correlation (r = 0.82) with organic matter. Nonetheless, the increase in CEC represents a relatively better nutrient condition for tree growth.

A significant positive correlation was observed between Al (double-acid extractable) in the bedded soil (SAL) and tree growth in Immokalee series (Table 3). The Al level was, however, low. Some reports (Mullette, 1975; Qureshi, 1978) have shown that small additions of Al to the growth medium have increased growth of some species of eucalypts. In this study, high levels of Al were associated with higher levels of Ca and P in the surface soil horizon, as well as with rates of GRP. The stratification of the data by levels of GRP showed that the effect of soil Al on tree growth depended on levels of GRP. The Al effects on growth were significant at the 1.0 ton/ha rate but not at the 2.0 tons/ha rate. It is possible that at the low rate of GRP, trees partially depended on P fixed by Al for their growth, while at the high rate of GRP, Al-phosphates were not an important source of P. Mullette et al. (1974) proposed that

at low Al concentrations, the Al ions block sufficient negatively charged sites of the cell wall material to facilitate entry of the negatively charged phosphate ions into the cell. At higher concentrations of Al, if the negative sites are supersaturated, then precipitation of the Al and the subsequent binding of P follows. The importance of Al-phosphates as a source of P for plant growth has also been indicated in other studies (Barros, 1974; Fassbender and Tschinkel, 1974; Humphreys and Truman, 1972) and mycorrhizae may be involved in the release of phosphate from these compounds.

Ground rock phosphate is not a soil chemical property, but its application increased the supply of soil P and Ca and apparently affected other soil nutrients. In addition, the increase of P in the soil solution could have inactivated part of the soil Al by forming Al-phosphates, thus favoring tree growth. The increase in rates (1 ton to 2 tons/ha) of GRP accounted for 19% of height growth and volume variation ($r = 0.44$) for the overall study area and for 52% of dominant height variation in Immokalee series.

The volume of wood per hectare increased 47% and height 19% in the Immokalee series as the rate of GRP was doubled.

An idea of the relative importance of the different horizons as a root feeding zone was given by comparing the number of chemical properties that were significantly correlated to tree growth in each soil series. It appeared that in the Immokalee series the A_1 horizon was relatively more important in tree nutrition than the A_2 and B_2h because 61% of the chemical properties significantly related to tree growth were in the A_1 horizon. In the Myakka series 54% of the chemical

properties related to growth were in the A_2 horizon and in Smyrna soil tree growth seemed to depend equally on properties of the A_1 and B_2h horizons.

Soil physical properties as related to tree growth

Tree mean height and wood volume in the study area were significantly higher on sites where the spodic horizon was deeper in the soil profile. The growth of the dominant trees was not, however, significantly affected by the depth to that horizon (Table 4). The depth to the spodic horizon was quite variable in the study area, ranging from 26 to 121 cm (Figure 5) with an average of 76 cm (Table A1). Increasing pine productivity in the coastal plains of the United States has frequently been related to increases in the effective depth of the soil profile (Linnartz, 1963; Ralston, 1951; Zahner, 1954), which is usually defined as depth to the least permeable horizon or depth to mottling. Barnes and Ralston (1955) found that yields of slash pine in Florida increased as the depth to the least permeable horizon increased to about 65 cm and depth to mottling to 87 cm but tended to decrease with further increases in depth to those zones.

In the present study, the relationship between tree height and depth to the B_2h horizon (Figure 5) was not well defined in the Immokalee series. However, it seemed that the best height growth tended to occur on soils with an average B_2h depth of about 90 cm. Karschon and Van Praag (1954) considered that the best depth to hardpan for growth of *E. camaldulensis* in Israel was about 100 to 125 cm. Usually the influence of subsoil depth on tree growth is expressed through its effect on the amount of growing space for tree roots and conditions of soil moisture and aeration.

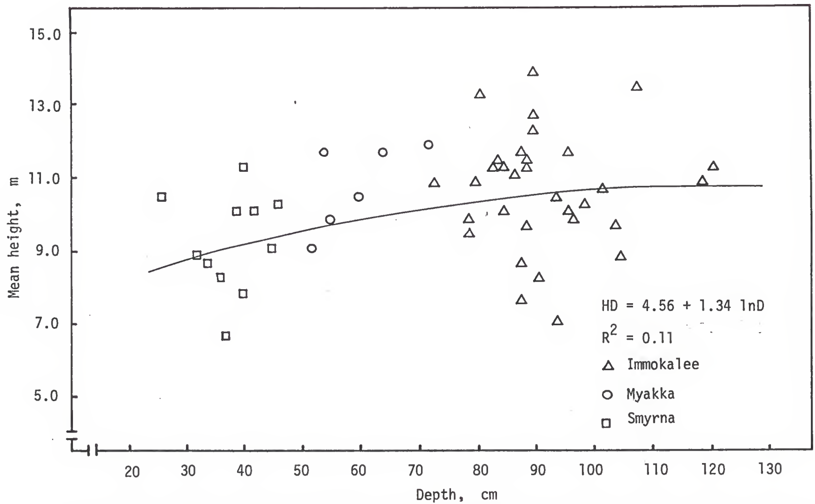

Figure 5. Relationship between depth to the spodic horizon and mean height of *E. grandis* in South Florida.

Table 4. Correlation coefficients between tree growth parameters and soil physical properties.

Soil physical property	Soil series														
	Immokalee (n = 32)				Myakka (n = 7)				Smyrna (n = 11)			Study area (n = 50)		
	HO(†)	HM	VOL	DM	HO	HM	VOL	OM	HO	HM	VOL	HO	HM	VOL
O(†)	(††)						0.76						0.32	0.36
A_1TH						0.81	0.84							
A_2TH											0.70		0.29	0.34
BTH	-0.39	-0.48	-0.37											
STR					-0.90									
SNB									-0.68					
CSNA					-0.90									
CSNB		-0.36		-0.40		-0.84	-0.84	-0.79						
FSNB									-0.67					
VFSNB	0.49	0.40		0.43								0.29		
SIB	-0.36	-0.44	-0.40	-0.40										
CLA		0.41		0.41										
CLB	0.43	0.39		0.40										
SICLB									0.68					
A2FC		0.40		0.42										
BFC										0.64	0.65			
BWP	0.52	0.39										0.39		
BWA										0.61	0.68			
DWTF						-0.81	-0.82	-0.77						

(†) Codes are defined in Table 2.

(††) Only significant values (<5% level) are shown.

In our study, the increase in eucalypt growth with increasing depth to the spodic horizon is presumably due to the greater volume of soil available for root exploitation and the effect of this horizon on soil moisture regime. Deeper soils could present a larger amount of soil nutrients for uptake by the feeding roots. In the study area, depth to the B_2h horizon was significantly correlated to thickness of both the A_1 ($r = 0.52$) and the A_2 ($r = 0.88$) horizons. The increase in the thickness of the A_1 horizon with B_2h depth is particularly important because most soil nutrients are concentrated in this horizon as well as a large portion of the feeding roots.

The effect of depth of the B_2h horizon on the moisture regime of the soil is determined by a number of characteristics of this horizon. For example, during the wet season there is no great effect of the B_2h horizon on the moisture regime because the water table is very close to the soil surface (Table A1) on all sites. During this time, parts of the root systems of trees are in a poorly aerated zone and a large portion of the roots in the A_2 may be killed. However, as the growing season advances evapotranspiration is intensified and the water table is progressively lowered. In the Smyrna soils, because the spodic horizon is thinner and softer, the water table drops below this layer very soon (Table A1). In this case, the supply of water for tree growth will depend on the capillary conductivity which is very restricted in sandy soils when they have low moisture content. Hence, it is quite possible that water deficiency occurs in the surface layers of the Smyrna soils as the growing season advances, with consequent water stress and reduction in tree growth.

The content of very fine sand (VFSNB) and moisture retention at 15 bars (BWP) of the B_2h horizon were the only other soil physical properties significantly correlated with tree growth in the overall area. The increase in the values of these two variables were associated with better height grwoth. These two properties were both closely related to clay and organic matter contents of the B_2h horizon. The positive influence of those soil properties on tree growth may be explained through their effect on a better soil moisture regime during dry seasons. The present results concur with those reported by Ralston (1951) who found that subsoils holding larger amounts of water were associated with better site quality for longleaf pine in the Atlantic Coastal Plain.

The effects of other soil physical properties on tree growth depended on soil series. The relative increase of coarser textural fractions in the A_1 and B_2h horizons was associated with reduction in tree growth, in the three soil series. Obviously the reverse was observed as the content of finer fractions increased (Table 4). These relations are in agreement with those reported for loblolly and slash pines in the Coastal Plain by several investigators (Barnes and Ralston, 1955; Linnartz, 1963; Zahner, 1954). The increase of coarse fractions in these soils reduces the water holding capacity with negative effects on tree growth. The importance of adequate water supply to site productivity in this study is corroborated by the positive correlation between moisture retention capacity at 0.1 and 15 bars and tree growth, and water availability in the B_2h horizon and tree growth in Immokalee and Smyrna series (Table 4).

The productivity of the Immokalee series was reduced by an increase in B_2h horizon thickness. The relationship between this soil property and tree mean height is shown in Figure 6. The relationship of this soil characteristic with tree growth is not in agreement with that reported by Shetron (1972) for red oak growing on Montcalm and Graycalm soils in Michigan. Increases in the thickness of the spodic horizon in our study presumably restricted root growth in this horizon due to reduced pore space and relatively high amounts of exchangeable Al($r = 0.34$).

The growth of dominant trees in the Myakka series was adversely affected by hardness of the spodic horizon. It should be pointed out that the number of observations on this series was very small but the above relationship was very well defined (Figure 7). The values of hardness reported herein are generally much higher than that reported by Brandon et al. (1977) for spodic horizons of Leon soils (Aeric Haplaquod). Coultas (1973) found that hardness of undisturbed cores of spodic horizons did not affect rooting depth or total root growth of seedlings of loblolly and slash pines. The hardness of his cores was, however, much lower (3.2 kg/cm^2) than those reported herein. Hardness of soil layer has been reported to reduce elongation and to cause abnormal growth of some agricultural plants (Davidson and Hammond, 1977; Fiskell et al., 1968).

While the reduction in the height of eucalypt trees in our Myakka soils was probably due to restriction to root growth, it is difficult to separate the effects of hardness from those of lack of aeration due to reduced porosity. For seven plots where the bulk

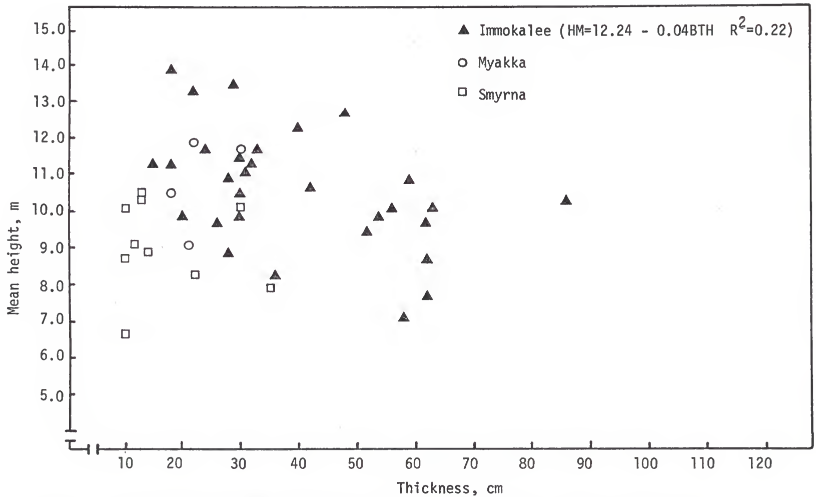

Figure 6. Relationship between thickness of the spodic horizon and mean height of *E. grandis* in South Florida.

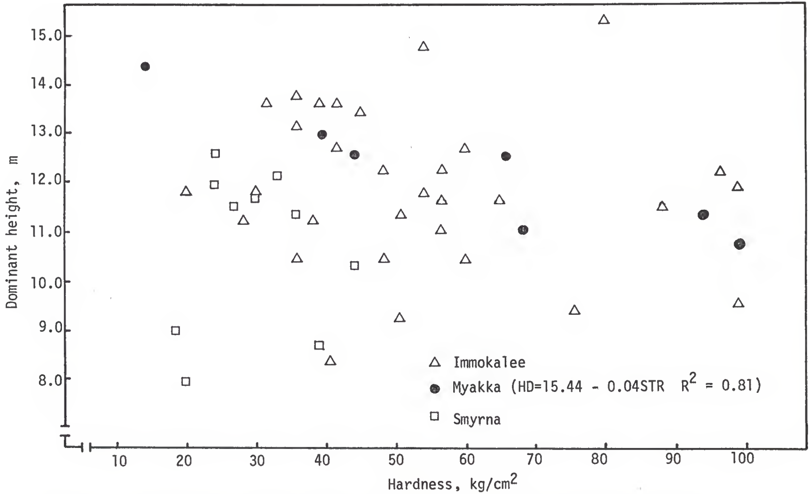

Figure 7. Relationship between hardness of the spodic horizon dominant height of *E. grandis* in South Florida.

density of the spodic horizon was determined, there was a significant correlation ($r = 0.78$) between hardness and bulk density.

The relationship between water table depth and tree growth was not as significant as expected. Significant correlations were obtained only between tree growth on the Myakka soils and the mean depth to the water table at the beginning of the summer (Table 4) and between tree growth and depth to the water table during the dry season of 1977 ($r = -0.78$). In both cases, the increase in depth of the water table was associated with decrease in growth, probably indicating a water deficit in the root zone.

The absence of a better correlation between tree growth and depth to the water table in this study may be due to the infrequent occasions on which the measurements were made. All the measurements were performed at a given point in time which may not have had any biological significance. Changes in the water table can take place in a very short time depending on solar radiation, precipitation, and vegetation density. Furthermore, it was assumed that measurements performed in 1977 and 1978 would reflect the effect of the water table on tree growth in the period between 1973 and 1977. It is accepted that forest stands can cause modification in the depth of shallow water tables. Therefore, water table measurements should be performed concomitantly with growth measurements over the entire rotation.

Tree Growth as Influenced by Multiple Soil Properties

The effects of two or more soil properties on eucalypt growth were studied by stepwise regression with the objective of establishing empirical growth predicting equations. Equations were calculated

first for the overall study area and then by soil series. Because of the small number of observations on Myakka and Smyrna series, equations were also calculated combining the data of these soil types.

Selected equations relating eucalypt growth to soil properties are listed in Table 5. Equations 1 and 3 in this table accounted for about 60% of height growth variation and equation 5 explained 55% of the variation in volume in the overall study area. The relationship of each soil property included in these regression equations with tree growth is basically the same as discussed in the previous sections.

Tree mean height in the overall area increased as the ratio between depth and thickness of the spodic horizon (D/BTH) increased (Figure 8). However, in the Immokalee soil this relationship was best expressed by a logarithmic equation ($HM = 9.16 + 1.48 \ln (D/BTH)$. On this soil, tree mean height increased as the D/BTH ratio increased to about 3.0 and then leveled off with further increases in the ratio. Thus, it appears that when values of this ratio are about 3.0, more favorable nutrient and moisture regimes exist for tree growth on the Immokalee soil. While the correlation coefficient ($r = 0.37$) between D/BTH and mean height was only significant at the 3% level, the regression coefficient in equation 3 was highly significant (at the 0.03% level). This indicates that the effect of this variable on tree height depended on the other variables in the latter equation.

The magnitude of possible dependences (i.e. collinearity) among the soil properties in equations 1, 3, and 6 was examined by ridge regression procedures. The use of some automatic procedures such as

Table 5. Selected multiple regression equations relating tree growth to soil properties.

Soil Series	Equation No.	Equation	F	R^2	$SEE^{(\sigma)}$	$E(R_0^2)$	$E'(R^2)$	$R^2_{Adj.}$	$1-\frac{SEE}{sy}$
IMS(†)	1	$HD = 27.08 - 4.13\ MPH - 0.27\ SAK + 0.45\ SOC^2 + 0.004\ O*VFSNB$	15.8	0.58	0.86	0.08	0.61	0.55	0.46
(n=49)	2(#)	$HD = 2.18 + 1.91\ MPH - 0.20\ SAK + 0.66\ SOC^2 + 0.007\ O*VFSNB$	27.0	0.36	1.30				
	3	$HM = 12.57 + 0.26\ SAL - 2.43\ BPH + 0.47\ CLB + 0.45\ O/BTH$	18.1	0.62	0.96	0.08	0.64	0.58	0.36
	4(#)	$HM = 4.90 + 0.28\ SAL - 0.98\ BPH + 0.75\ CLB + 0.60\ O/BTH$	24.1	0.33	1.30				
	5	$VOL = -121.03 + 14.45\ SOC + 23.81\ \ln O + 2.49\ O/BTH + 1.97\ SAL$	13.9	0.55	0.92	0.08	0.58	0.51	0.30
I	6	$HD = 8.40 + 0.38\ SAL + 0.01\ BKAL + 0.14\ FF - 4.00\ \log BTH$	20.9	0.76	0.85	0.13	0.78	0.72	0.47
(n=32)	7(#)	$HD = 11.82 + 4.44\ SAL + 0.12\ BKAL + 2.30\ FF - 19.89\ \log BTH$	54.1	0.64	0.97				
	8	$HM = 4.55 - 0.04\ BTH + 0.42\ SAL + 0.14\ ANA - 10^{-4}\ SOCKG$	24.5	0.78	0.79	0.13	0.80	0.75	0.50
	9	$VOL = 70.84 + 2.28\ SAL - 2.72\ BFC + 3.77\ SOC^2 - 28.56\ \log BTH$	9.8	0.59	0.92	0.13	0.64	0.53	0.32
MS	10	$HD = 16.18 - 0.20\ A_1P - 0.64\ CSNB$	23.8	0.77	0.70	0.12	0.78	0.76	0.49
(n=17)									
	11	$VOL = -42.59 + 0.93\ SMG + 0.10\ SP^2 + 139.94\ \log O(BPH)$	46.9	0.92	0.35	0.19	1.00	0.90	0.68
IMS	12	$HD = 27.67 - 1.13\ BPH + 0.10\ SP - 3.44\ A_1PH + 0.44\ SOC^2$	11.5	0.51	1.18	0.08	0.53	0.44	0.25
(n=49)	13	$HD = 5.54 + 0.02\ A_2TH + 0.52\ VFSNB + 0.85\ BWP + 20.42\ \log STR$	6.4	0.37	1.27	0.08	0.41	0.31	0.17
	14	$HD = 17.15 + 0.21\ SMG + 20.90\ \log D/BTH - 1.98\ BPH + 0.58\ VFSNB - 0.45\ SAK$	11.8	0.58	1.05	0.10	0.62	0.53	0.35
	15	$HM = 7.81 - 0.04\ BTH + 0.21\ SAL + 4.36\ \log D - 2.58\ BPH + 10^{-3}\ BAL + 0.43\ VFSNB$	14.4	0.67	0.91	0.12	0.71	0.63	0.58
I	16	$HD = 14.45 + 0.28\ SAL - 0.55\ SK - 2.50\ \log BTH + 0.46\ VFSNB$	19.0	0.74	0.88	0.13	0.75	0.70	0.45
(n=32)	17	$VOL = 48.33 + 2.85\ SAL - 24.15\ \log BTH$	10.8	0.43	1.05	0.13	0.49	0.34	0.22
S (n=10)	18	$HM = 7.15 + 0.65\ O/BTH + 22.87\ VCSNB$	17.2	0.83	0.52	0.22	0.85	0.78	0.53

(†) IMS=All soil series combined; I=Immokalee, MS-Myakka and Smyrna combined; S=Smyrna
(σ) SEE is expressed in m for HD and HM and in m^3/ha for VOL.
(#) The regression coefficients were calculated by ridge regression.

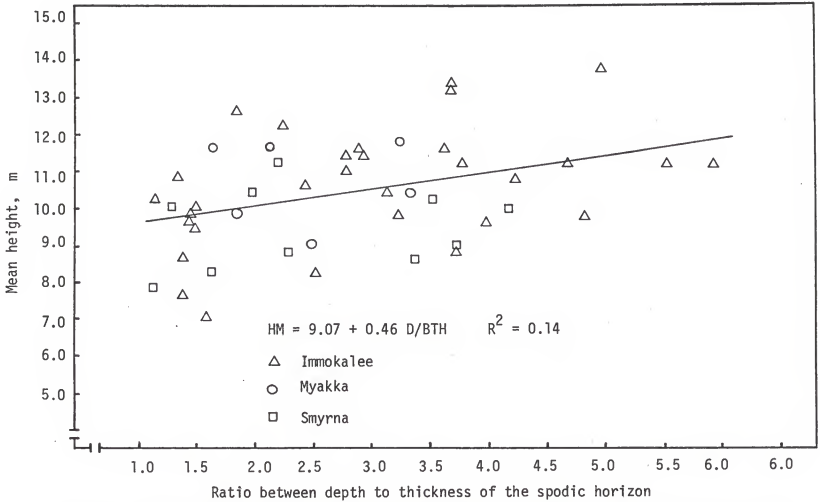

Figure 8. Relationship between the ratio of depth to thickness of the spodic horizon and mean height of *E. grandis* in South Florida.

stepwise and best regressions attempt to untangle the variables by selecting some "best" subsets of the predictor variables. However, these procedures do not necesarily reduce predictor variable correlations. Therefore, if these variables are not orthogonal, the least square coefficients may be inflated and unstable in that their values and their signs change erratically from one sample to another (Ung, 1978). The use of such equations may not produce reliable predictions if the estimation data show large changes in relation to those used for calculating the coefficients. The ridge regression reduces the effect of multicollinearity and gives stable regression coefficient (i.e., not sensitive to small changes in the estimation data) although they are biased (Ung, 1978).

The regression coefficients calculated by ridge regression are shown in equations 2, 4, and 7 (Table 5). As indicated by the reduction in the R^2 values of equations 1 and 3, the collinearity among the soil properties in each of these equations caused an increase in the R^2 value (i.e., increases in the variance of the equation) of about 22 and 29%, respectively. The relationship between the observed mean height and that predicted by equation 4 is shown in Figure 9. The fact that soil properties are not truly independent of each other is well recognized and has been the focus of criticism of the use of soil-site regressions as a tree growth predicting tool. The effectiveness of equations 1 and 3 in predicting height of *E. grandis* probably will be satisfactory only in areas where similar relationships among the soil properties included in each of these equations are observed.

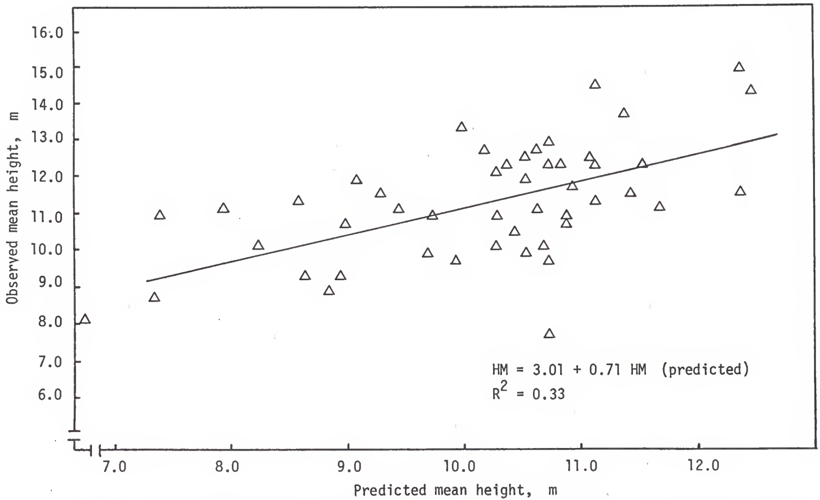

Figure 9. Plot of the mean height predicted by equation 4 in Table 5 against the observed mean height of *E. grandis* in South Florida.

The dominant height, as predicted by equation 7, was plotted against the observed height, as shown in Figure 10. This figure and the comparison between the R^2 values of equations 6 and 7 indicate that equation 6 can produce reliable prediction of height growth of *E. grandis* in other areas of Immokalee soils.

As indicated before, the coefficient of determination (R^2) was a criterion used to select equations. Fowler and Bigelow (1979) discussed the problems associated with the use of R^2 values as an indicator of usefulness, goodness-of-fit, or predictive precision in natural resource studies. These authors stated that when evaluating a single regression equation, comparing different regression equations from the same set of data or from different sets of data, causal relationships or predictive precision cannot be determined solely by looking at R^2 and the significance of the regression equations. A regression equation with a high R^2 could have lower predictive precision than a regression equation with a lower R^2 if the higher R^2 is associated with a steeper slope. Another problem associated with the use of R^2 is when no relationship exists between the dependent and independent variables in the population, and a very high R^2 is obtained by chance, especially when the number of independent variables in the equation approaches the number of observations.

The statistical variables proposed by Fowler and Bigelow (1979) for evaluating regression equations were calculated for most of the equations listed in Table 5. These parameters

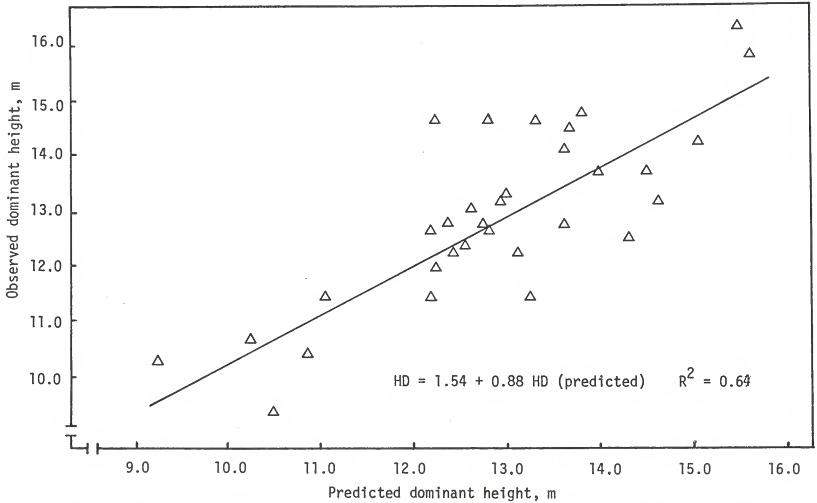

Figure 10. Plot of the dominant height predicted by equation 7 in Table 5 against the observed dominant height of *E. grandis* in South Florida.

indicated that most equations in Table 5 are very significant. The R^2 values are considerably larger than E (R_0^2)—the expected R^2 when no true relation between dependent and independent variables existsin the population and E'(R^2)—the expected R^2 when the R^2 in the population is equal to R^2 obtained by the regression equation, indicating that the probability of R^2 being as large by chance is negligible. Also, the $R^2_{Adj.}$ and the term 1-SEE/sy indicate that a major portion of the variation in tree growth is explained by the regression equations. The $R^2_{Adj.}$ values for all the equations were significant at the 1% level.

Considerable improvement in the predictive precision was obtained when equations were calculated by soil series. This improvement probably was a consequence of eliminating the variation associated with soil series. Most of the variation in tree growth could be explained by one or two soil properties in the Myakka and Smyrna series. However, one should keep in mind that the number of observations in these two soil series was very small. Some of the linear regressions calculated for these soil series are listed in Table A4. Some growth prediction equations calculated by combining the data of Myakka and Smyrna series are also presented in Table 5. In these equations a relatively small number of soil properties gave a reasonably high R^2 value. Hence, in evaluating *E. grandis* productivity, Myakka and Smyrna series may be combined without great reduction of predictive precision.

The intent in including equations 12 and 13 (Table 5) was to give an indication of the relative importance of physical and chemical properties in predicting tree growth. It is obvious from those equations that height of *E. grandis* in the area was more closely related to chemical properties than to soil physical properties. However, the combination of chemical and physical properties provided the best growth predicting equations.

Equations 14, 15, 16, and 17 are also composed of soil properties considered to be easily determined in the field and in the laboratory.

It was evident from the previous sections that the application of ground rock phosphate to the area caused changes in the nutrient regime of the soil and that eucalypt growth was significantly affected by the rates applied. Thus, additional equations (Table 6) were calculated, (1) including the rates of GRP as an independent variable and (2) stratifying the data by GRP rates. The point to be made by the equations in the first half of Table 6 is that doubling the rate of GRP significantly increased eucalypt growth in the area. This emphasizes the original condition of P deficiency of these soils.

The equations at the lower half of Table 6 predict tree growth within each level of GRP application. It should be mentioned that only selected soil properties were included for computing those equations. The regression equations for the overall study area and for the Immokalee series confirm the importance of organic matter as a soil factor positively influencing tree growth. Increasing surface soil K was associated with increases in the mean height of the trees in the overall area indicating the soils are likely K deficient. In

Table 6. Regression equations relating tree growth to soil properties as influenced by rates of ground rock phosphate (GRP).

Soil Series	Equations	F	R^2	SEE(††)
	Effect of GRP included			
IMS(†)	HO = 12.51 - 1.22 BPH + 2.08 SOC - 0.45 CSNB + 10^{-3} GRP + 0.32 O/BTH	14.2	0.63	0.98
(n=49)	HM = 19.99 - 3.34 MPH + 0.91 BOC + 0.21 BMG - 0.38 CSNB + 10^{-3} GRP	12.5	0.59	1.01
	VOL = -23.44 + 19.51 SOC + 0.28 D - 3.46 CSNB + 0.01 GRP	13.6	0.55	9.00
I	HO = 9.16 + 1.88 SOC - 0.55 CSNB + 2 x 10^{-3} GRP	30.4	0.76	0.82
(n=32)	VOL = 127.65 - 34.69 MPH + 20.84 SOC - 2.61 CECB + 10^{-3} GRP	11.0	0.62	0.88
	Effect of GRP corrected			
	1.0 ton GRP/ha			
IMS	HO = 11.04 + 1.74 SOC - 0.44 CSNB	16.3	0.51	0.90
(n=34)	HM = 12.65 + 0.36 SAK + 1.24 BOC + 0.09 AITH - 0.83 CSNB	12.4	0.63	0.81
I	HD = 12.70 + 1.09 BOC - 0.65 CSNB	18.1	0.68	0.72
(n=20)	HM = 11.15 + 0.99 BOC - 0.72 CSNB	16.1	0.66	0.80
	2.0 tons GRP/ha			
IMS	HO = 54.86 - 10.78 MPH + 0.25 BMG	20.5	0.77	0.86
(n=15)	HM = 35.99 - 6.99 MPH + 0.37 BMG	11.9	0.66	1.01
I	HO = 13.43 + 1.20 SOC - 0.03 BTH	8.1	0.64	0.66
(n=12)				

(†) IMS=All soil series combined; I=Immokalee.
(††) SEE is expressed in m for HD and HM and in m^3/ha for VOL.

the section of the plantation receiving 2.0 tons GRP/ha, tree height growth was better in areas where the content of Mg in the spodic horizon was higher. Among other possible reasons, the positive effect of Mg on tree growth might be related to plant P metabolism (Epstein, 1972). At high levels of P, plants need a relatively higher amount of Mg for their normal growth. The inverse relationship between surface soil pH and tree growth on the same section of the area indicates an indirect effect presumably through its interaction with soil organic matter and improved rates of GRP dissolution,as pointed out before. Sites with better water holding capacity favored tree growth, as indicated by the negative effect of increasing coarse sand fraction in the spodic horizon.

In summary, the results of this study showed that the variation in growth of *E. grandis* in the area cannot be explained by a single physical or chemical soil property. The multiple regressions indicated the biotic and/or abiotic factors not determined in this study have a reasonable effect on tree growth. Soil properties explained 60 to 70% of eucalypt growth variation according to the criteria of statistical significance adopted.

Relationships of Foliar Element Concentrations to Soil Elements and Tree Growth

Nitrogen

Foliar N concentrations tended to be negatively related to tree growth on all soils (Table 7) although the coefficients were not statistically significant except for tree dominant height in the Immokalee soil and for volume and diameter in the Myakka soil. The range

Table 7. Correlation coefficients between tree growth parameters and foliar element concentrations.

Soil Series	Growth Parameter	N	P	K	Ca	Mg	Na	Al	Mn	Cu
IMS(†)	HD	-0.17	0.29*	-0.04	-0.17	-0.07	0.24	-0.36**	-0.46**	-0.19
(n=50)	HM	-0.22	0.37**	0.02	-0.23	-0.03	0.11	-0.37**	-0.49**	-0.13
	VOL	-0.24	0.40**	0.06	-0.20	-0.02	0.24	-0.30*	-0.33*	-0.05
	DM	-0.26	0.43**	0.06	-0.24	-0.03	0.10	-0.30*	-0.49**	-0.17
I	HD	-0.37*	0.37**	-0.40*	-0.09	0.05	0.31	-0.54**	-0.59**	-0.31
(n=32)	HM	-0.25	0.33*	-0.44**	-0.21	0.01	0.20	-0.50**	-0.69**	-0.32
	VOL	-0.19	0.37*	-0.33*	-0.20	0.01	0.38	-0.40*	-0.57**	-0.20
	DM	-0.20	0.41*	-0.34*	-0.19	-0.05	0.11	-0.41*	-0.71**	-0.30
M	HD	-0.72	0.25	0.32	-0.28	0.08	0.71	-0.29	-0.15	-0.34
(n=7)	HM	-0.72	0.67	0.86*	-0.02	0.42	0.42	-0.57	-0.17	-0.24
	VOL	-0.77*	0.66	0.84*	-0.01	0.54	0.54	-0.51	-0.03	-0.23
	DM	-0.83*	0.60	0.75*	-0.19	0.53	0.53	-0.55	-0.05	-0.35
S	HD	0.18	-0.03	0.49	-0.32	-0.46	-0.04	0.11	-0.49	0.01
(n=11)	HM	-0.06	0.31	0.57	-0.48	-0.38	-0.16	0.21	-0.43	0.19
	VOL	-0.25	0.51	0.46	-0.35	-0.40	-0.05	0.21	-0.01	0.41
	DM	-0.23	0.45	0.61	-0.52	-0.21	-0.08	0.31	-0.31	0.23

(†) IMS=All soil series combined; I=Immokalee; M=Myakka; S=Smyrna.

* Significant at the 5% level. ** Significant at the 1% level.

of leaf N concentration was relatively narrow (1.02 to 1.44%) and extremely low as compared with the critical level (2.22%) found by Haag et al. (1961) for *E. grandis*. The increase in foliar N concentrations has been positively correlated with better growth of *E. deglupta* (Lamb, 1977), *E. saligna* (Mello, 1968), and other eucalypt species (Haag et al., 1976). The low levels of foliar N in the present study confirm the results of the soil analysis which indicated that the soils in the area are N deficient. In fact, in a trial carried out on *E. grandis* plantations located in an area near the present study, Barros and Pritchett (1978) found significant increases in height and diameter increments in response to N applications. The overall increase in height increment in response to the fertilizers was 38% over of that of unfertilized control.

The negative correlations between foliar N and soil concentrations of P, Ca, and Mg (Table 9) were difficult to interpret because many plant and environmental factors interfere with N uptake. For example, in the Immokalee soils, leaf N concentrations were negatively correlated with rates of GRP. The faster growth resulting from the application of 2.0 tons GRP/ha was not accompanied by proportional plant N uptake, hence suggesting a dilution effect.

Phosphorus

The increase in foliar P concentration was associated with better tree growth and its relationship with eucalypt mean height is shown in Figure 11. The P concentrations were generally higher than the critical level (0.17%) for *E. grandis* (Haag et al., 1961) as well as for other eucalypt species (Haag et al., 1976; McColl and Humphreys,

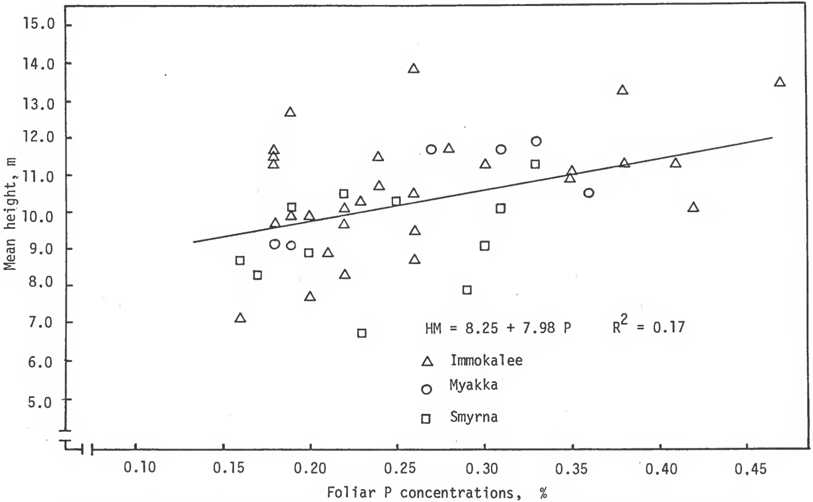

Figure 11. Relationship between foliar P concentrations and mean height of *E. grandis* in South Florida.

1967; Mello, 1968). The values presented herein are, however, comparable to those reported by Barros and Pritchett (1978) for N-fertilized *E. grandis* growing on the same type of soils which were not considered P deficient.

In spite of the improved eucalypt growth with increasing foliar P concentrations, it appears that P is not growth limiting factor on the soils of the study area. The relationship of foliar P to tree growth could in part be representing an indirect effect because of the synergism among foliar P, Ca, and K concentrations (Table 8).

Increases in surface soil P content were associated with increases in foliar P concentrations (Table 9). The same relationship was observed between foliar P and rates of GRP and soil Ca and Al, whereas the reverse occurred between foliar P and soil K. Positive correlations between foliar P and soil P and foliar P and soil Ca have also been observed for other eucalypt species (McColl, 1969; McColl and Humphreys, 1967). The positive relationship between foliar P and soil Ca indicates that P uptake is closely related to the amount of Ca available in the rhizosphere. Calcium is very important in root elongation and in maintaining the integrity of the cell membrane and its deficiency in the growth medium results in deranged cell division. In addition, Ca counteracts the effect of low pH in the medium and has an important protective role when potentially damaging ions are present in the medium at high concentrations (Epstein, 1972). The negative relationships between soil Ca and leaf Al and Mn (Table 9) indicate that soil Ca somehow reduced the uptake of Al and Mn by the trees.

Table 8. Correlation coefficients between foliar element concentrations.

Foliar element	Soil series	Foliar elements K	Ca	Al	Mn	Cu
N	I(†)	(††)		0.67		0.46
P	IMS	0.38	0.28			
	M	0.88				
K	I				0.36	
	S					0.70
Ca	IMS				0.40	
	I				0.38	
	S			-0.63		
Mg	M				0.79	
	S			-0.75		
Al	IMS					0.32
	I					0.40
Mn	IMS					0.32
	S					0.63

(†) I=Immokalee; IMS=All soil series combined; M=Myakka; S=Smyrna

(††) Only significant values (<5% level) are shown.

Table 9. Correlation coefficients between foliar element concentrations and surface soil element concentrations.

Soil element	Soil series	Foliar element concentrations								
		N	P	K	Ca	Mg	Na	Al	Mn	Cu
(ppm)		-------	-------	-------	%	-------	-------	-------	ppm	-------
N	IMS(†)	(††)								-0.32
	M								-0.79	
	S									-0.64
P	IMS		0.28							
	I	-0.39					-0.35	-0.37	-0.45	
	M			0.80						
	S								-0.67	
K	IMS		-0.29			-0.29		0.44		
	I	0.42	-0.44					0.58	0.49	0.36
	M						-0.81			
Ca	I	-0.35					-0.44	-0.39	-0.36	
	M		0.70	0.93				-0.90		
	S		0.82						-0.66	
Mg	IMS				-0.31					
	I								0.44	0.39
	M	-0.79								
Na	M						0.89			
	S	0.85								
Al	IMS		0.32	-0.30					-0.43	
	I		0.55					-0.54	-0.50	
	M					-0.78		-0.93	-0.79	
GRP (σ)	IMS		0.44				0.34	-0.45		
	I	-0.48	0.42					-0.68		

(†) IMS=All soil series combined; M=Myakka; S=Smyrna; I=Immokalee.
(††) Only significant values (<5% level) are shown.
(σ) Ground rock phosphate.

The negative relationship between leaf P and soil K was influenced by the GRP rates. When the data were stratified by GRP rates, this relationship was not significant. The positive correlations between foliar P and foliar K (Table 8) and between soil P and leaf K (Table 9) also indicated that these relationships were influenced by GRP.

The positive correlation between leaf P and soil Al supports the hypothesis that Al at low levels is somehow important in eucalypt P nutrition, as suggested by Mullette et al. (1974).

Potassium, Calcium, and Magnesium

The relationship between tree growth and foliar K concentrations differed among soil series. These two factors were negatively correlated on Immokalee, positively correlated on Smyrna, and significantly correlated on the Myakka series (Table 7). However, when the data of the Myakka and Smyrna series were combined, the relationship between leaf K and mean height was very significant (r = 0.69). The relationship between eucalypt mean height and foliar K concentrations for all soil areas is illustrated in Figure 12. The foliar K concentrations found in this study ranged from 0.43 to 0.67% and were much lower than the critical level (1.14%) reported by Haag et al. (1961) for leaves of 2-year-old *E. grandis*. The average concentration for the overall study area was 0.54% (Table A2) and also lower than that (0.58%) found by Haag et al. (1976) for plants of the same species showing K deficiency symptoms. The low levels of K in both soil and leaves in the present study indicate that a growth response to K fertilizer applications is quite probable.

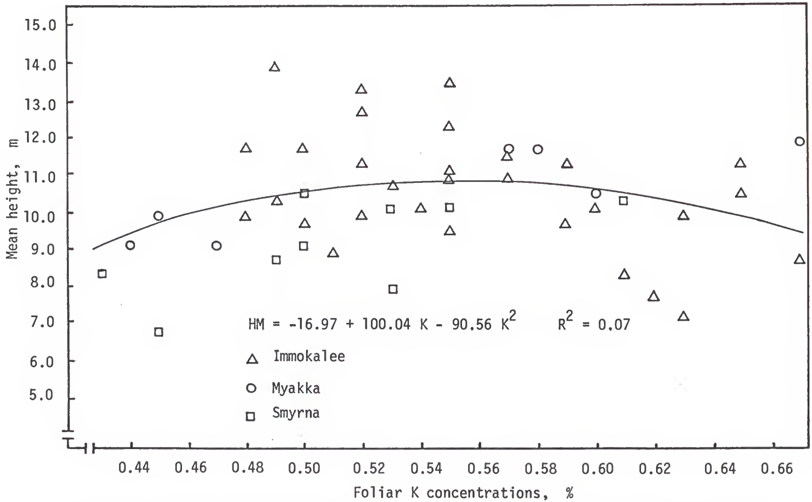

Figure 12. Relationship between foliar K concentrations and mean height of *E. grandis* in South Florida.

Tree growth was not significantly related to foliar Ca and Mg concentrations (Table 7). The concentrations of Ca in the leaves ranged from about 0.75 to 1.40% and those of Mg from 0.28 to 0.37%. The critical foliar concentrations of Ca and Mg for *E. grandis* was reported (Haag et al., 1961) to be 1.14% and 0.44%, respectively. However, in another study, Haag et al. (1976) found a nonsignificant relationship between volume of eucalypts and foliar Ca and Mg, even when the concentrations were as low as 0.54% and 0.17%, respectively. Furthermore, the application of lime to eucalypt plantations has not resulted in significant growth increases (Knudson et al., 1970; Mello, 1968). Hence, it appears that, in spite of the marginal foliar Ca and Mg concentrations, Ca and Mg are not limiting tree growth in the study area.

Foliar Ca concentrations were inversely correlated with surface soil Mg content, while the foliar concentrations of Mg were negatively related with soil K and Al contents. These inverse correlations seem to indicate an antagonistic effect of the element in the soil on plant uptake of the other. Similar relations have been reported by several investigators (Epstein, 1972; Harward et al., 1955; McColl, 1969) for other plants.

Other Elements

An inverse relationship was observed between foliar Mn concentrations and tree growth in the overall area and in the Immokalee soil (Table 7). The relationship between Mn concentrations and tree mean height is shown in Figure 13. These Mn concentrations are much lower than those reported by other investigators (Haag et al., 1976; McColl

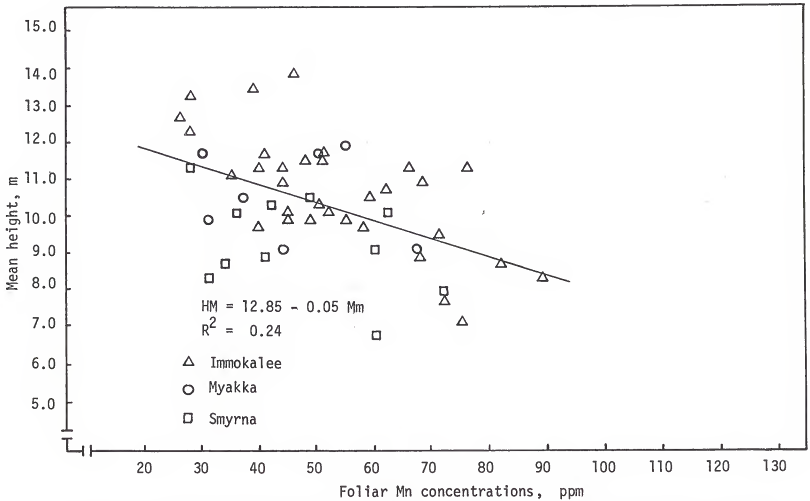

Figure 13. Relationship between foliar Mn concentrations and mean height of *E. grandis* in South Florida.

and Humphreys, 1967) for other species of eucalypts. In Brazil, *E. grandis* growing on acid Latosols contained 446 ppm Mn in the leaves but wood production was not affected by this element (Haag et al., 1976).

The average foliar Mn concentration of *E. grandis* in the present study is about half of that of foliage of loblolly and slash pine plantations (Kaufman et al., 1977; White and Pritchett, 1970) growing on flatwood soils in Florida. The critical level of foliar Mn for *E. grandis* has not been established but the levels reported herein do not seem to be sufficiently high to be toxic to trees. The statistical analysis performed by stratifying the data by GRP showed that the inverse correlation between tree growth and foliar Mn concentrations was independent of GRP rates. Hence, the decrease in eucalypt growth with the increase of foliar Mn concentrations probably reflects an indirect effect of other factors, possibly an internal imbalance of nutrients or a reduction in Mn uptake as a result of GRP applications.

Foliar Mn concentrations increased with increasing foliar concentrations of K, Ca, and Mg (Table 8) showing an apparent synergism.

The relationship between foliar Al concentrations and tree growth followed the same pattern as that between foliar Mn and tree growth (Table 7). The leaf Al concentrations ranged from 50 to 100 ppm. Not much information is available regarding Al concentrations in eucalypt leaves but they are generally lower than in pines (Haag et al., 1961; Humphreys and Truman, 1964). Humphreys and Truman (1972) suggested that this difference is because the eucalypts have a mechanism for rejecting Al^{3+}. Qureshi (1978) indicated that *E. saligna* seedlings

accumulated, to a certain extent, Al in old leaves, i.e., up to 378 ppm Al.

The critical level of foliar Al for *E. grandis* has not been established but the levels reported herein do not seem to be sufficiently high to be toxic to trees.

Foliar Al concentrations were negatively correlated with double-acid extractable Al in the Immokalee and Myakka soils (Table 9). This relation does not agree with those reported by Humphreys and Truman (1972) for radiata pine seedlings and by Qureshi (1978) for *E. saligna* seedlings, for which Al uptake was a direct function of the level of Al^{3+} in the growth medium. In our study, surface soil Al was significantly and positively correlated with soil Ca and P and rates of GRP. Therefore, Ca could have interfered with plant Al uptake. In fact, the correlation between soil Ca and leaf Al was negative.

No significant relationship existed between foliar Na or foliar Cu concentrations and tree growth (Table 7). Sodium concentrations ranged from 0.12 to 0.26% and Cu concentrations from 1 to 8 ppm. These Na concentrations are similar to those reported by McColl and Humphreys (1967) for four eucalypt species but are much higher than that reported by Raupach and Clarke (1978) for needles of radiata pine. Feller (1978) also reported that *E. regnans* and *E. obliqua* added larger amounts of Na to the soil than *Pinus radiata* and *Pseudotsuga menziesii*, through litter fall. Thus, it appears that eucalypts are Na-accumulators.

The average foliar Cu concentration (4.5 ppm) in this study was slightly lower than that reported by Haag et al. (1976) for *E. grandis*

in Brazil but was higher than that for slash pine growing on a Spodosol in Florida (Kaufman et al., 1977). The critical foliar Cu level for *E. grandis* is not yet known but for *E. tereticornis* it is around 10 ppm. However, in a greenhouse study* *E. grandis* did not respond to micronutrient applications when the growth medium was an A_1 horizon soil collected from a Spodosol in southern Florida. Therefore, Cu is unlikely a growth limiting factor for *E. grandis* in the study area.

Multiple Regressions Relating Tree Growth with Foliar Nutrient Concentrations

The relationships between tree growth and foliar nutrient concentrations were additionally examined by multiple regression analysis including the quadratic term of each element (to allow for possible curvilinear relations) and products and ratios between elements (to allow for possible interactions). The relationship between tree height and foliar P was best expressed by a simple linear equation as indicated in Figure 11. However, the relationship between volume (m^3/ha) and leaf P concentration was best represented by a quadratic model (Table 10) which gave an improvement in the R^2 value of 8% as compared to the linear model. For all other elements when the relationship was significant, it was best expressed by linear models.

The data were further analyzed by stepwise regression in order to obtain models that could predict tree growth using foliar concentrations. Equations were calculated for the overall area and for

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* Duncan, D. V., personal communication.

Table 10. Regression equations relating tree growth and foliar element concentrations.

Soil series	Equations	F	R^2	SEE(†)
IMS(††)	1 HD = 14.83 - 0.16 Al - 0.04 Mn + 4.87 P/Ca	9.1	0.37	1.32
(n=50)	2 HM = 11.94 - 0.15 Al - 0.04 Mn + 6.38 P/CA	12.2	0.44	1.21
	3 VOL = 42.23 - 144.37 P + 385.81 P^2	7.4	0.24	11.70
I	4 HD = 17.93 + 4.72 P - 0.26 Al - 0.04 Mn - 7.53 K^2	13.8	0.67	1.00
(n=32)	5 HM = 16.80 + 30.31 P/Al - 0.05 Mn - 8.61 K	21.3	0.70	1.00
	6 VOL = 50.53 + 213.02 P/Al - 0.43 Mn	12.4	0.46	10.20
MS	7 HD = 11.07 - 54.11 Mg^2 + 13.12 K	5.9	0.44	1.26
(n=18)	8 HM = 4.90 - 40.63 Mg^2 + 17.24 K	14.6	0.66	0.89
	9 VOL = 20.70 - 16.12 N*Ca + 103.98 K^2	10.0	0.57	7.90
S	10 HD = 6.39 - 57.56 Mg^2 + 22.45 K	7.2	0.64	1.06
(n=11)	11 HM = 3.25 - 43.54 Mg^2 + 20.71 K	7.4	0.65	0.89

(†) SEE is expressed in m for HD and HM and in m^3/ha for VOL.

(††) IMS=All soil series combined; I=Immokalee; MS=Myakka and Smyrna combined; S=Smyrna.

individual soil series (Table 10). The effects of each element on tree growth in the equations listed in Table 10 are consistent with that shown by the correlation coefficients. For the overall area, the best growth prediction was obtained for mean height (equation 2) for which the foliar concentrations of Al, Mn, and the ratio between P and Ca accounted for 44% of the variation. Likewise for the relationship between tree growth and soil nutrients, improvement on the R^2 values was obtained by stratifying the data by soil series.

In summary, soil and foliar levels indicated that N and K are deficient in the area. The soils seem to have an adequate P supply. Although the concentrations of both Ca and Mg were at marginal levels, they are unlikely growth limiting factors in the study area. In spite of the low foliar levels, Al and Mn were significantly and inversely related with tree growth. This may be a consequence of possible imbalances in the internal nutrient concentrations.

Effects of Levels of Aluminum Applied to Spodic Horizon Soil on *E. grandis* Seedlings

A greenhouse trial was conducted to test the hypothesis that the level of exchangeable Al in the spodic horizon reduces *E. grandis* root development and penetration into this layer and to establish the approximate level of Al toxicity to roots.

Effects of Al Levels on Seedling Growth

Symptoms of Al toxicity appeared on seedlings growing in pots with the highest level (625 ppm) of Al within two weeks after the experiment started. In some pots, the leaf tips dried and the seedlings were stunted for a long time. Where the symptoms were

most severe, the leaves showed progressive wilting and they were completely dried four weeks after treatment. The young leaves were generally narrow and small. Seedlings planted in pots treated with 125 ppm Al also showed leaves with dried tips and necrotic spots appeared on the older leaves. These symptoms are somewhat similar to those described by Qureshi (1978) for Al toxicity on *E. saligna* seedlings.

Height growth increments as a function of levels of Al application are shown in Figure 14. This figure shows that the application of Al up to 25 ppm, in addition to the native exchangeable Al (125 ppm) of the spodic horizon, did not affect seedling height growth. Growth of plants in pots treated with 125 ppm Al was somewhat reduced up to 2 months after treatment application, whereas virtually no growth occurred in pots which received 625 ppm Al up to this time. At this time, soil samples collected from pots receiving the highest level of Al and in which the seedlings had died, contained about 300 ppm of exchangeable Al.

Two and one-half months after treatment application the pots were lightly flushed with deionized water on the suspicion of chloride toxicity.

From Figure 14, it seems clear that part of the substances detrimental to tree growth in pots treated with 125 and 625 ppm Al was removed by flushing. Even so, the development of the roots was drastically reduced at the end of 5 months (Table 11). This indicates that root systems damaged due to Al toxicity present slow recoveries at high Al applications.

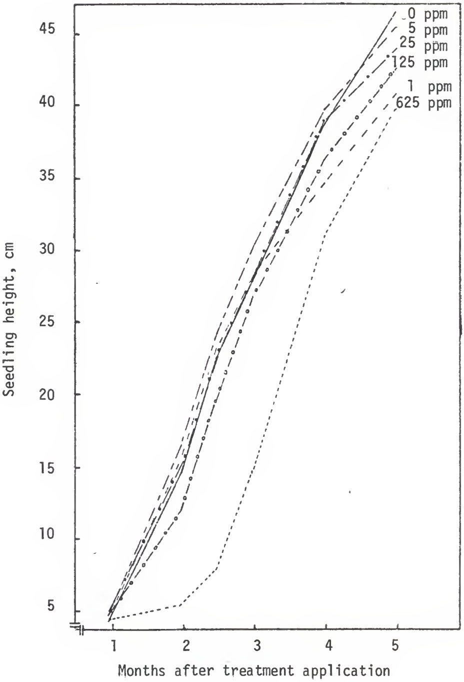

Figure 14. Height growth of *E. grandis* seedlings as influenced by levels of Al (ppm) applied to potted spodic horizon soil.

Table 11. Effects of levels of Al applied to the B_2h soil on growth parameters of *E. grandis* seedlings.

Applied Al	Mean height	Shoot weight		Root weight						Plant total dry weight
				Fresh		Dry		Total		
		Fresh	Dry	A_1	B_2h	A_1	B_2h	Fresh	Dry	
ppm	cm	g								
0	46.6a*	78.6a	31.2a	36.1b	35.4a	9.4b	6.1a	71.6ab	15.5ab	46.7ab
1	40.8ab	76.6a	31.6a	53.6a	23.2bcd	13.0a	4.2bc	76.8ab	17.2a	48.7a
5	45.5ab	80.4a	32.7a	36.0b	26.2abc	10.1ab	4.6ab	62.2b	14.7ab	47.4ab
25	44.1ab	75.1a	28.7a	53.0a	33.4ab	10.7ab	4.8ab	86.4a	15.5ab	44.2ab
125	42.6ab	62.9a	24.7a	36.2b	18.5cd	8.7b	2.9cd	54.7bc	11.6b	36.3b
625	39.8b	34.1b	13.4b	22.8b	11.5d	4.1c	1.6d	34.2c	5.7c	19.1c

* Values followed by the same letters are not statistically different at the 5% level.

Values of seedling growth parameters assessed 5 months after treatment application are shown in Table 11. The reduction in shoot weight was a result of the severe leaf shedding caused by the application of 625 ppm Al. The detrimental effects of the applications of 125 and 625 ppm Al on plant growth may be explained by their toxic effects on root development and apparent depressing effects of Al on N, P, and Ca uptake (Table 14). The increase of Ca in the medium was associated with better seedling growth (Table 14) presumably by suppressing Al activity.

Effects of Al Levels on Seedling Elemental Composition

Seedling shoot elemental composition as influenced by the Al levels applied to the B_2h horizon soil is shown in Table 12.

The differences in N, K, Mg, Zn, and Cu concentrations, as affected by Al levels, were the consequence of a dilution effect.

The high concentrations of Mn in shoots of seedlings grown in pots with low levels of Al were due to the better root development of these plants (the r value between root weight and shoot Mn concentration was 0.79). Furthermore, high levels of Al in the soil might have reduced Mn plant uptake. Shoot Mn concentrations were negatively correlated with both exchangeable ($r = -0.55$) and extractable ($r = -0.50$) Al in the soil.

Generally, the most marked differences in root nutrient concentrations were caused by the highest level of Al application (Table 13). The application of 625 ppm of Al to the spodic soil tended to reduce

Table 12. Effects of levels of Al applied to the B_2h soil on the elemental concentration of *E. grandis* shoots.

Applied Al	N	P	K	Ca	Mg	Al	Mn	Fe	Zn	Cu
ppm	%					ppm				
0	0.89ab*	0.23a	0.71b	1.1a	0.20ab	77a	373a	30a	47abc	3.0a
1	0.91ab	0.29a	0.72ab	1.2a	0.22a	65a	342a	33a	45abc	3.7a
5	0.83b	0.24a	0.69b	1.0a	0.18b	78a	332a	32a	41bc	3.5a
25	0.92ab	0.28a	0.75ab	1.2a	0.21ab	103a	337a	38a	54a	4.3ab
125	0.97a	0.25a	0.80a	1.1a	0.19b	105a	280b	37a	51ab	5.7bc
625	0.90ab	0.26a	0.80a	1.1a	0.20ab	62a	210c	35a	37c	6.8c

* Values followed by the same letters are not statistically different at the 5% level.

Table 13. Effects of levels of Al applied to the B_2h soil on elemental concentrations and contents of *E. grandis* roots in the A_1 and B_2h soils.

Applied Al	N	P		K		Ca		Mg		Al		Mn		Fe		Zn		Cu	
	$A1+B_2h$	A1	B_2h	A1	B_2h	A1	B_2h	A1	B_2h	A1	B_2h	A1	B_2h	A1	B_2h	A1	B_2h	A1	B_2h
										Elemental concentration									
--ppm--		%								ppm									
0	0.94ab*	0.17b	0.32ab	0.30a	0.54a	0.47c	0.24a	0.13a	0.12a	350c	2630a	23a	19bc	170ab	57a	220ab	160b	10	3a
1	0.96a	0.20ab	0.31ab	0.28a	0.43a	0.60a	0.23a	0.12a	0.10a	480bc	2330ab	20a	15c	260a	57a	250a	210ab	14bc	4a
5	0.80b	0.18b	0.28ab	0.29a	0.47a	0.53bc	0.23a	0.13a	0.10a	330c	1750b	24a	20bc	140b	53a	180b	190b	10c	3a
25	0.93ab	0.22ab	0.34a	0.29a	0.44a	0.48b	0.23a	0.12a	0.10a	480bc	2583a	19a	26ab	210ab	65a	280a	230ab	20a	3a
125	0.85ab	0.21ab	0.31ab	0.32a	0.51a	0.41d	0.23a	0.12a	0.10a	580ab	2300ab	19a	29ab	170ab	53a	260a	270a	18ab	6b
625	0.78b	0.22ab	0.24b	0.31a	0.41a	0.38d	0.26a	0.14a	0.10a	780a	3100a	26a	32a	170ab	92b	260a	300a	18ab	8c
										Elemental content									
		g								mg									
0	14.58ab	1.62b	1.94a	2.83b	3.27a	4.37bc	1.43a	1.18b	0.72a	3.29b	1.60a	0.21a	0.11a	1.62b	0.34a	2.06bcd	0.99a	0.10d	0.02a
1	16.29a	2.60a	1.33ab	3.57a	1.74b	7.73a	1.03ab	1.59a	0.42bc	6.53a	1.03ab	0.25a	0.06b	3.47a	0.24ab	3.31a	0.82ab	0.18ab	0.02a
5	11.65bc	1.76b	1.28ab	2.91b	2.14b	5.33b	1.07ab	1.27ab	0.46bc	3.42b	0.81b	0.24a	0.10ab	1.38b	0.24ab	1.79cd	0.83ab	0.10cd	0.02a
25	14.46ab	2.32a	1.64ab	3.11ab	2.15b	5.14bc	1.12ab	1.28ab	0.51ab	5.21ab	1.25ab	0.20ab	0.12a	2.32ab	0.31a	2.98ab	1.10a	0.22a	0.01a
125	9.81c	1.79b	0.91bc	2.77b	1.48bc	3.56c	0.68b	1.07b	0.30bc	5.04ab	0.67b	0.17ab	0.08ab	1.47b	0.16b	2.21bc	0.79ab	0.15bc	0.01a
625	4.42d	0.89c	0.36c	1.28c	0.62c	1.60d	0.41b	0.58c	0.16c	3.21b	0.48b	0.11b	0.05b	0.71b	0.14b	1.09d	0.46b	0.07d	0.01a

* Values followed by the same letters are not statistically different at the 5% level.

Table 14. Correlation coefficients between soil chemical properties and growth parameters and between soil chemical properties and elemental concentrations of *E. grandis* roots in the A_1 and B_2h soils.

		Soil chemical characteristics											
		pH		Double-acid extractable								N KCl extractable	
		N KCl(1:1)		P		Ca		Mg		Al		Al	
Seedling		A_1	B_2h	A_1	B_2h	A_1	B_2h	A_1	B_2h	A_1	B_2h	A_1	B_2h
							Growth parameters						
Shoot weight													
Fresh		(†)		-0.67	0.52		0,69			-0.61	-0.73	-0.54	
Dry				-0.69	0.55		0.70			-0.60	-0.74	-0.58	
Root weight													
Fresh	A_1										-0.57		
	B_2h			-0.49						-0.50	-0.49		
Dry	A_1	-0.53	-0.76	-0.60			0.48				-0.74	-0.52	
	B_2h			-0.58			0.59			-0.57	-0.58		
							Root composition						
N	A_1+B_2h			-0.56						-0.61	-0.52	-0.57	
P	B_2h		-0.54	-0.48						-0.48			
K	B_2h				0.53		0.53						
Ca	A_1	-0.54	-0.69				0.54				-0.49		
Al	A_1	0.57	0.76			-0.56	-0.68			0.50	0.50		
	B_2h							0.50			0.50		0.71
Mn	B_2h	0.64	0.63				-0.51						
Fe	B_2h		0.75	0.80		-0.71	0.74	0.73		0.65	0.74	0.74	0.70
Zn	B_2h		0.74	0.58	-0.50		-0.51			0.58	0.59	0.48	
Cu	B_2h	0.55	0.94	0.76	-0.53	-0.58	-0.78			0.79	0.85	0.64	

(†) Values are shown only where the relationship is significant at the 5% level.

the N and B_2h root P concentrations. Calcium concentrations in roots growing in the A_1 soil were severely reduced by the application of 125 and 625 ppm Al. The reduction in the concentrations of these elements was consistent with the root biomass of plants of these two treatments. Besides the possible Al interference on the uptake of those elements, lower root concentrations of N, P, and Ca at the highest level of Al application were also a result of the smaller volume of soil exploited by the plants.

Aluminum concentrations in roots growing in both A_1 and B_2h soils were proportional to the amount of Al in the soil (Table 14). However, Al taken up by the plants was not translocated to a great extent. There was an increasing gradient in Al concentrations from shoots to roots growing in the B_2h soil. Therefore, it appears that eucalypts, in fact, have a mechanism in the roots that prevents Al translocation to the tops, as suggested by Humphreys and Truman (1972).

Roots growing in the B_2h soil had higher concentrations of P, K, and Al than those in the A_1 soil. The higher P and Al concentrations in the B_2h suggest the formation and precipitation of Al-phosphates in that part of the roots. Foy et al. (1978) listed examples involving several plant species in which Al-phosphate precipitates were observed in the roots. The precipitation of Al-phosphates in the roots may constitute the mechanism by which eucalypts prevent translocation of high amounts of Al to the top.

Roots growing in the A_1 soil contained higher Ca, Mg, and Cu concentrations than roots in the B_2h soil. Calcium and Mg concentrations in the A_1 and B_2h soil were very similar. Therefore, the low concentrations of these elements in roots growing in the B_2h soil are presumably due to restriction on their uptake imposed by the higher levels of Al in that soil layer.

In summary, the results of this trial indicated that growth of both shoots and roots of *E. grandis* trees would be significantly reduced when planted on soils whose spodic horizon contains about 300 ppm of exchangeable Al. Therefore, it is likely that Al concentrationsin the spodic horizons in south Florida will restrict growth and development of roots into these layers. The reduction in root growth probably would not have much effect on shoot nutrient concentrations. Furthermore, it was shown that shoot Al concentrations of *E. grandis* are not good indicators of the Al concentrations in the roots and in the soil.

The Eucalypt Root System

Root systems of seven *E. grandis* trees were excavated to characterize the gross morphology of the roots and to examine root growth and distribution as affected by depth and thickness of spodic horizons. The results reported herein were obtained in two studies, one performed in September 1978 and the other performed in June 1979.

Eucalyptus grandis growing on Spodosols in South Florida presented a very distinctive tap root form (Figure 15). Many eucalypt species have been reported to develop prominent tap root systems, particularly on drier areas (Cremer et al., 1978). However, for some

Figure 15. Taproots (in an upside down position) of a 6-year-old *E. grandis* tree growing on a Haplaquod in South Florida.

species such as *E. regnans*, the tap root remains prominent only during early years and subsequently sinker roots become important (Ashton, 1975). Whether *E. grandis* ever develops sinker roots has not been reported. In any event, the development of such roots was not evident in our study. The diameter of the tap root just below the soil surface tended to be approximately equal to that of the stem at the base of the tree. The taproot usually divided at about 50 cm below the soil surface giving origin to two or more smaller taproots. These smaller taproots extended downward to a depth corresponding to that of the spodic horizon. These taproots were virtually deprived of lateral branching and tapered very sharply as they approached the spodic horizon (Figure 15).

In almost every plot, the taproot penetrated the spodic horizon but for only a few centimeters (about 7.0 cm). The roots in the spodic had a very small diameter (about 2.0 mm) and showed little branching.

The first-order lateral roots originated just below the soil surface (Figure 16) and tended to grow horizontally within 20 to 30 cm of the surface soil. In many cases, when growing along the beds, they penetrated beneath the closest neighbor tree. When growing across the row, they extended to about 2.0 to 2.5 m from the trunk. The diameters of roots in this class were a function of their number and size of the tree. Diameters of about 10 cm close to the stump were not uncommon for the largest laterals. However, these roots tapered very fast and branched at about 1.0 m from the stump giving origin to second-order laterals with diameters of about 3.0 cm or less.

Figure 16. Partial exposure of a 5-year-old *E. grandis* root system growing on a Haplaquod in South Florida.

Other root classes were limited to the A_1 (including the bed) and A_2 horizons (Figure 16). The largest portion of the fine roots (<2.5 mm) was confined to the bed and A_1 horizon forming, along with larger roots, a very dense mat. Mycorrhizal development was observed on this class of roots, particularly in the top few centimeters of the surface soil.

In every plot, fine and large roots (except taproots) showed abrupt termination in the A_2 horizon in a "brush-like" appearance (Figure 16). High percentages of dead and decaying roots were found in this horizon and were attributed to an oxygen deficiency caused by the periodic high water table levels. The taproot growing in this horizon showed no strong evidences of damage due to poor aeration. Therefore, tapering close to the spodic horizon and the inability of the taproot to penetrate and develop into this layer to any great extent, appears to be caused by spodic characteristics such as reduced pore space and high levels of exchangeable Al. The bulk densities of the spodic horizons in the plots where roots were excavated varied from 1.51 to 1.80 g/cm^3 (Table A7) and tree roots apparently encountered some difficulty in penetrating this "hardpan" layer. The concentrations of exchangeable Al in the same horizons were, in all plots but one, above 250 ppm. Therefore, some Al toxicity is likely to occur and, at least partially, to restrict root development in the spodic horizon in the study area.

Trees were taller and produced larger amounts of roots in soils of intermediate depth than in soils with deep or shallow spodic horizons (Table 15). The amount of roots in soils with shallow

Table 15. Height and fresh weight (FW) of the above-ground trees and weight and percent distribution of dry roots as affected by depth of the spodic horizon.

Spodic depth	Plot No.	Tree height	Tree Fw	Soil horizon	Root classes					
					Fine		Large		Total	
(cm)		m	kg		ton/ha	%	ton/ha	%	ton/ha	%
<50	5	12.2	59	A_1	4.3	33.7	8.4	66.3	12.7	(74.3)[(†)]
				A_2	1.4	30.7	3.0	69.3	4.4	(25.7)
					5.7	(33.3)	11.4	(66.7)	17.1	
50-75	1	13.6	71	A_1	9.5	45.3	11.4	54.7	20.9	(84.9)
				A_2	1.4	39.0	2.3	61.0	3.7	(15.1)
					10.9	(44.3)	13.7	(55.7)	24.6	
>75	2,3	12.9	75	A_1	3.0	14.4	17.8	85.6	20.8	(88.9)
	4,6			A_2	1.0	38.5	1.6	61.5	2.6	(11.1)
					4.0	(17.1)	19.4	(82.9)	23.4	

(†) Numbers in parentheses represent percentage over the total of roots in each depth class.

spodic horizons, i.e., less than 50 cm deep, was about 30% less than in soils with deeper horizons. Since the roots did not effectively penetrate the spodic horizon, the reduced growth of trees on the shallow soils may be explained by the smaller volume of soil available for root exploitation as well as by the influence of this horizon on the water table. In the study area, shallow spodic horizons were thinner ($r = 0.46$) and softer ($r = 0.41$) than the deep ones. Therefore, shallow spodic horizons may not perch the water table for long periods. In fact, the level of the water table just after the growing season started tended to be below the 50 cm depth (Table A1). With further decreases in the water table, the supply of water for tree growth on shallow soils will depend on the upward capillary movement. Hence, it seems likely that water deficiency will occur in the surface layer of these soils, resulting in water stress and reduced tree growth during the extended dry periods common to the region.

The weight of large roots was greater than that of fine roots in all of the soil depth classes. The best balance between the two root classes was observed on soils with the spodic horizon at intermediate depths (Table 15). This was associated with the largest total amount of roots and the greatest tree height growth.

Root distribution as a function of thickness of the spodic horizon (Table 16), generally followed the same kind of trend as observed for depth of the horizon. However, the differences in root biomass between classes of thickness were not as large as observed for depth classes. This indicates that the thickness of the spodic horizon was relatively less important on root biomass production than the depth of the spodic.

Table 16. Height and fresh weight (FW) of the above-ground trees and weight and percent distribution of dry roots as affected by thickness of the spodic horizon.

Spodic thickness	Plot No.	Tree Height	Tree FW	Soil horizon	Root classes					
					Fine		Large		Total	
(cm)		m	kg		ton/ha	%	ton/ha	%	ton/ha	%
<20	3,5	13.0	69	A_1	4.2	24.3	13.1	75.7	17.3	(84.0)(†)
				A_2	1.3	39.4	2.0	60.6	3.3	(16.0)
					5.5	(26.7)	15.1	(73.3)	20.6	
20-40	1,6	13.0	70	A_1	6.5	30.2	15.0	69.8	21.5	(87.8)
				A_2	1.0	33.3	2.0	66.7	3.0	(12.2)
					7.5	(30.6)	17.0	(69.4)	24.5	
>40	2,4	12.0	76	A_1	2.2	11.2	17.4	88.9	19.6	(88.3)
				A_2	1.0	38.5	1.6	61.5	2.6	(11.7)
					3.2	(14.4)	19.0	(85.6)	22.2	

(†) Numbers in parentheses represent percent over the total of roots in each thickness class.

The anchorage of a tree is highly dependent on the balance between the weight of the above-ground portion and that of the root system. Assuming a green moisture content of 55% (Franklin, 1977) for the above ground tree, the shoot:root ratio in our study varied from 1.6 to 2.1 with an average of 1.8. Giordano (1967) found for *E. globulus* in Italy, a ratio of about 3.0 when the fresh weights of both components were used. It appears that the conditions in the study area favored *E. grandis* to produce relatively more roots than reported in Giordano's study.

Weight of the above-ground part of the tree was a better indicator (r = 0.96) of the total root dry weight than tree height (r= 0.82). The following equation relates total root dry weight (TRDWT) to the above-ground fresh weight (SFWT) of the tree:

TRDWT = -0.201 + 0.317 SFWT, with a R^2 = 0.98, which is significant at 1% probability level.

SUMMARY AND CONCLUSIONS

The relationships among tree growth, foliar elemental concentrations, and soil physical and chemical properties were examined in a 4-year-old *E. grandis* plantation growing on a Haplaquod in southern Florida, for the purpose of identifying those soil properties of greatest importance to tree growth. Site preparation included webbing, chopping, and bedding. One ton of ground rock phosphate (GRP) per hectare was applied to 3/4 of the plantation and 2.0 ton/ha to the other 1/4 of the area. Tree measurements and leaf and soil samples were taken from fifty 120 m^2 plots allocated proportionally to the area of the three soil series identified on the site. Thirty-two plots were on the Immokalee, seven on the Myakka, and eleven on the Smyrna soil series. Soil samples were collected from the bed and major soil horizons to 2 m depth. The leaf samples were analyzed for N, P, K, Ca, Mg, Al, Mn, Na, and Cu. The soil samples were chemically analyzed for pH; total N; total and extractable P; extractable K, Ca, Mg, Na, Al, Fe; organic carbon; and CEC. Soil physical analyses included texture and moisture holding capacity determinations. Additionally, field determinations of depth, thickness, and hardness of the spodic horizon, and depth to the water table were performed. Root systems of seven trees were excavated to characterize the gross morphology of the roots and to examine the effect of depth and thickness of the spodic (B_2h) horizon on root biomass and distribution. Finally,

a greenhouse trial was conducted to study the effect of Al applied to a potted B_2h soil on root penetration and development into this spodic horizon.

In the overall study area, tree growth was smaller than that obtained for the same species in other countries. This was probably due to the generally poor soil and site conditions for tree growth, i.e., high acidity, low levels of nutrients, high level of exchangeable Al in the B_2h horizon, and the unfavorable soil moisture regime. Tree growth was better on the Immokalee and Myakka soils than on the Smyrna soils. There were significant increases in tree growth of 19% and 47% for height and volume, respectively, when the rate of GRP was increased from 1.0 to 2.0 tons/ha on the Immokalee soil.

The relationships between tree characteristics and soil properties were examined by regression analysis, considering first the data for the overall study area and then for each soil series separately. Dominant and mean tree heights and volume of wood per hectare constituted the dependent variables for the regression analysis. Surface soil pH was the chemical property most closely correlated with tree growth in the overall area and accounted for about 30% of height growth variation. The inverse relationship between this soil property and tree growth represented an indirect effect through its interrelationship with other soil features, presumably, content of organic carbon in the surface soil and content of P in the spodic horizon, and due to its effect on the rate of GRP dissolution.

The increase of soil organic matter content was associated with better tree growth. Soils richer in organic matter presented, in turn,

higher contents of N, K, Ca, and Mg and higher values of CEC and water-holding capacity. Similarly, tree growth was better on sites where the spodic horizon had the higher P contents and largest CEC.

Surface soil Ca was positively correlated with diameter growth but the correlation of surface soil K and Mg content with tree growth, whether positive or negative, varied with soil series. The correlations between these elements and tree growth were positive for the Myakka and Smyrna soils and negative for the Immokalee soil. The relationships for this latter soil were, however, affected by the rate of GRP that had been used and were no longer significant when the data were stratified according to GRP rate. Therefore, it appeared that the increase in the GRP rate resulted in a decrease of surface soil K and Mg.

In the Immokalee soil, the increase of double acid-extractable Al at the lower rate of GRP was associated with better tree growth. This relationship was interpreted as an indication of the partial dependence of tree P nutrition on the presence of Al phosphates.

Tree growth increased as the depth of the spodic horizon increased to about 90 cm then growth leveled off with further increases in depth. This was attributed to the greater volume of soil available for root exploitation for nutrients and water, particularly during drier periods.

In general, tree growth was positively correlated with soil properties indicative of higher water-holding capacity such as fine textural fractions and water holding capacities between 0.1 and 15 bars suction.

The increases in the thickness and hardness of the spodic horizon were associated with decreased tree height growth in the Immokalee and Myakka soils, respectively.

In the overall area and in the Immokalee soil, tree growth was positively correlated with foliar P concentrations but negatively correlated with foliar Al and Mn concentrations. The relationship between tree growth and foliar K concentration was positive in the Myakka but negative in the Immokalee soil. In this latter soil, the relationship was negative due to a dilution effect. Foliar P concentration increased with increasing soil P content but the reverse was observed for the relationship between foliar Al and soil Al.

Soil and foliar N and K values were very low indicating a probable deficiency of these elements in the study area. Hence, eucalypt growth responses to the application of N and K fertilizers would be expected. The levels of soil and leaf Ca and Mg were marginal but are unlikely growth limiting factors in the area. In spite of the positive correlation between foliar P concentration and tree growth, both soil and leaf P levels appeared to be adequate for normal tree growth.

The best growth predicting equations from soil properties accounted for about 60% of height growth and 55% of volume growth in the overall study area. Stratifying the data by soil series resulted in R^2 values no lower than 0.76 in any of the soil types. Combining the data for Myakka and Smyrna soils produced equations that accounted for 86% of mean height growth variation and 92% of volume variation. Ridge regression procedures showed that, in some of the growth prediction equations, the multicollinearity among soil variables included in the

model was responsible for a large portion of the R^2 values. Therefore, these equations may produce reliable growth prediction only when applied to the same area, or in areas with similar relationships among the soil properties included in the equations.

The greenhouse trial indicated that growth of shoot and roots of *E. grandis* will be substantially reduced when the levels of exchangeable Al in the spodic horizon are above about 300 ppm. Increasing the levels (0, 1, 5, 25, 125, and 625 ppm) of Al applied to the spodic soil had little effect on shoot elemental concentrations but affected root P, Ca, Mg, and Cu concentrations. The higher P and Al concentrations of roots growing in the B_2h soil than in the A_1 soil suggested the formation and precipitation of Al-phosphates in that part of the roots. This may constitute the mechanism by which eucalypts exclude or avoid translocation of high amounts of Al to the leaves. In the present study, roots in the B_2h soil contained up to about 0.31% Al. The lower concentrations of Ca, Mg, and Cu in roots growing in the B_2h soil than in the A_1 soil appeared to indicate a restriction on their uptake imposed by the higher levels of Al in the spodic horizon soil.

The root system study showed that *E. grandis* growing in south Florida presents a distinct tap root form. Most of the roots (75 to 85% of the total root biomass) are confined to the A_1 surface soil horizon. This is apparently due to a better nutrient and oxygen status of this layer than in the A_2 horizon, where a periodic high water table may result in considerable root mortality. The water table perches on the spodic horizon for significant periods during times

of extended rainfall. While the taproot of this species penetrated the A_2 horizon, it failed to effectively penetrate the spodic layer. This failure of the taproot to grow in the organic pan could be caused by a number of factors in addition to poor aeration. These factors include high bulk density (about 1.70 g/cm^3) and high exchangeable Al concentrations (about 280 ppm). It was noted that the root system biomass in the Smyrna (shallow spodic) was about 30% less than root systems in soils with deeper spodic horizons (Immokalee had 23 ton/ha and Myakka had 25 ton/ha of dry roots). These factors, no doubt, contribute to a severe water stress in trees growing on the Smyrna soil during extended periods when the water table is below the shallow spodic horizon but not below the deeper spodic horizons of other soils.

The results of this study seem to justify the following conclusions regarding eucalypt growth on south Florida Haplaquods:

1. No single soil property was responsible, by itself, for the large variation in *E. grandis* growth in the study area. Soil pH; contents of organic matter, K, and Mg; percentage of coarse sand in the spodic horizon; and depth and thickness of the spodic horizon were the most important soil properties affecting tree growth.

2. Soil and foliar analyses indicated deficiencies in N and K, therefore, eucalypt growth responses may be expected from applications of N and K fertilizers. The levels of P were apparently adequate for tree growth, whereas those of Ca and Mg were marginal.

3. Tree growth was better on the Immokalee and Myakka soils than on the Smyrna soil. Because this difference in growth was not solely explained by depth to the spodic horizon, other soil properties

are assumed to exert significant effects on tree growth. Furthermore, soil properties important for tree growth on one soil type were not necessarily important on the other soils. For example, the thickness of the spodic horizon significantly and negatively affected tree growth on the Immokalee soil, whereas the hardness of the same horizon was negatively related to tree growth on the Myakka soil.

4. Ground rock phosphate applied at the rate of 2.0 ton/ha increased tree growth on the Immokalee soil over growth associated with 1.0 ton GRP/ha.

5. Generally, soil chemical properties affected tree growth more strongly than physical properties. However, the best prediction equations contained both soil physical and chemical properties.

6. Factors other than those examined in this study, considerably influenced tree growth since the best growth predicting equations accounted for no more than 73% of tree height variation. However, equations considered most useful (those containing the more easily determined factors) accounted for about 60% in height growth variation and 55% in volume growth variation in the overall area. Stratifying the data by soil series improved the R^2 values. For practical purposes, data from Myakka and Smyrna soils can be combined for predicting tree growth.

7. The concentration of eucalypt root systems in the A_1 surface soil horizon was determined by the more favorable nutritional and aerational status of this layer. On the other hand, the taproot failed to effectively grow in the spodic horizon due to the poor aeration, high bulk density, and high concentration of exchangeable Al in this

horizon. In the Smyrna soil, these factors, associated with the limited volume of exploitable soil, contributed to a reduced root biomass. Therefore, a severe water stress for tree growth on this soil may occur during long dry periods when the water table is below the spodic horizon.

APPENDIX

Table A1. Soil chemical and physical properties of Immokalee, Myakka, and Smyrna soils.

Soil properties	Soil horizon	Immokalee Mean	Immokalee S.E.	Myakka Mean	Myakka S.E.	Smyrna Mean	Smyrna S.E.	Study area Mean	Study area S.E.
Chemical									
ph(H_2O) 1:2	Bed	3.7	0.11	3.8	0.20	3.8	0.14	3.8	0.14
	A_1	3.7	0.16	3.8	0.14	3.8	0.21	3.8	0.17
	A_2	4.3	0.27	4.3	0.36	4.1	0.28	4.3	0.30
	B_2h	3.4	0.15	3.7	0.39	4.3	0.27	3.6	0.43
pH(N KCl) 1:1	A_1	2.7	0.28	2.7	0.15	2.9	0.32	2.8	0.28
	8_2h	2.9	0.26	3.2	0.23	3.9	0.34	3.2	0.46
Org. carbon (%)	Bed	1.72	0.31	2.23	0.41	1.89	0.32	1.83	0.37
	A_1	1.45	0.50	1.82	0.33	1.44	0.36	1.50	0.46
	A_2	0.12	0.03	0.22	0.14	0.30	0.10	0.17	0.10
	B_2h	2.16	0.47	1.89	0.37	1.83	0.51	2.05	0.48
N (ppm)	A_1	455.00	123.00	683.00	146.00	519.00	178.00	501.00	158.00
	B_2h	364.00	95.00	459.00	97.00	593.00	189.00	428.00	152.00
P (ppm)	8ed	5.2	4.2	4.3	3.4	7.2	3.6	5.6	4.0
	A_1	4.6	6.9	2.0	1.5	7.2	7.4	4.8	6.6
	A_2	0.2	0.2	0.2	0.1	0.4	0.1	0.3	0.2
	8_2h	3.0	2.9	1.1	0.4	0.8	0.4	2.3	2.5
K (ppm)	Bed	3.9	0.9	4.2	0.5	3.7	1.4	3.9	1.0
	A_1	2.7	0.8	3.3	0.7	2.8	0.9	2.8	0.8
	A_2	0.8	0.3	1.0	0.2	1.2	0.2	0.9	0.3
	B_2h	0.9	0.3	1.0	0.2	1.7	0.5	1.1	0.5
Ca (ppm)	8ed	60.6	15.7	63.8	10.9	77.8	28.0	64.8	19.6
	A_1	37.8	23.0	41.4	18.0	45.8	22.8	40.1	22.2
	A_2	11.6	2.2	12.6	3.7	13.4	1.8	12.1	2.5
	B_2h	11.3	2.1	12.2	2.4	11.7	2.5	11.5	2.2
Mg (ppm)	Bed	7.1	1.1	10.1	3.6	8.0	4.3	7.7	2.7
	A_1	4.6	4.4	6.9	5.5	5.4	2.3	5.1	4.2
	A_2	1.1	0.3	2.2	1.9	2.1	1.0	1.5	1.0
	8_2h	4.1	2.4	4.2	1.6	3.1	1.3	3.9	2.1
Al (d.a.) (ppm	Bed	8.7	2.4	11.0	1.0	12.0	3.0	9.7	2.8
	A_1	7.4	4.0	10.7	2.4	10.1	3.6	8.5	3.9
	A_2	1.3	0.7	2.1	1.8	3.2	1.1	1.8	1.2
	B_2h	149.3	62.7	172.3	37.8	344.7	70.0	195.5	100.7

Table A1. continued

Soil properties	Soil horizon	Immokalee Mean	Immokalee S.E.	Myakka Mean	Myakka S.E.	Smyrna Mean	Smyrna S.E.	Study area Mean	Study area S.E.
Al(N KCl)	A_1	10.8	7.7	25.3	26.2	14.0	6.7	13.5	12.5
(ppm)	B_2h	145.1	48.6	141.6	45.8	89.7	54.2	132.4	53.6
Fe	A_1	6.9	2.0	9.5	4.1	11.3	6.6	8.2	4.2
(ppm)	B_2h	2.6	1.2	3.5	1.5	11.3	11.2	4.7	6.3
Na	A_1	42.5	4.2	45.1	5.0	42.5	3.7	42.9	4.2
(ppm)	B_2h	53.2	12.3	62.3	14.0	51.6	9.2	54.1	12.2
Total P	A_1	50.2	41.8	38.4	6.5	56.4	41.1	49.9	38.5
(ppm)	B_2h	60.4	54.6	53.4	5.6	81.2	22.1	64.0	45.6
CEC	A_1	2.5	1.2	3.7	1.6	2.7	0.9	2.7	1.3
(meq/100g)	B_2h	7.6	2.0	6.8	1.5	5.0	2.2	6.9	2.2
Physical									
Depth	A_2	24.0	3.0	23.0	4.0	20.0	4.0	23.0	4.0
(cm)	B_2h	93.0	10.0	58.0	7.0	38.0	6.0	76.0	25.0
Thickness	A_1	24.0	3.0	23.0	4.0	20.0	4.0	23.0	4.0
(cm)	A_2	69.0	14.0	35.0	13.0	18.0	7.0	53.0	23.0
	B_2h	39.0	18.0	25.0	6.0	17.0	8.0	32.0	17.0
Hardness (kg/cm^2)	B_2h	53.2	21.0	61.3	30.0	29.5	8.0	49.1	22.8
Sand	A_1	96.2	0.7	95.5	0.9	95.4	0.6	95.9	0.8
(%)	B_2h	92.9	1.0	93.0	0.8	92.2	1.1	92.8	1.0
Very coarse sand	A_1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
(%)	B_2h	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Coarse sand	A_1	6.9	2.3	7.3	2.3	5.9	1.3	6.8	2.2
(%)	B_2h	4.7	1.1	4.5	1.3	3.8	0.7	4.5	1.1
Medium sand	A_1	71.5	3.6	72.8	3.9	72.0	3.2	71.8	3.4
(%)	B_2h	62.2	2.8	64.1	1.3	65.0	2.1	63.1	2.8
Fine sand	A_1	19.0	4.3	17.6	3.9	19.3	2.6	18.9	3.9
(%)	B_2h	28.5	2.5	26.2	1.1	26.4	1.7	27.7	2.4
Very fine sand	A_1	2.4	1.0	2.2	0.9	2.6	1.0	2.4	1.0
(%)	B_2h	4.4	1.1	5.1	0.8	4.7	0.7	4.6	1.0
Silt	A_1	1.6	0.7	1.9	0.9	2.2	0.6	1.8	0.8
(%)	8_2h	1.5	0.7	1.2	0.6	1.0	0.8	1.3	0.7

Table A1. continued

Soil properties	Soil horizon	Immokalee Mean	Immokalee S.E.	Myakka Mean	Myakka S.E.	Smyrna Mean	Smyrna S.E.	Study area Mean	Study area S.E.
Clay (%)	A_1	2.3	0.7	2.6	0.3	2.4	0.5	2.3	0.4
	B_2h	5.6	0.9	5.8	0.8	6.7	0.7	5.9	0.9
Water retention (%) 0.1 bar	A_1	4.7	1.4	5.8	1.8	5.1	1.1	5.0	1.4
	A_2	1.5	0.2	1.9	0.7	2.4	0.6	1.7	0.5
	B_2h	8.2	1.5	7.9	2.1	7.6	1.7	8.0	1.6
15 bars	A_1	2.8	0.7	3.8	1.1	3.3	0.6	3.1	0.8
	B_2h	3.1	0.9	3.1	0.6	3.4	0.7	3.2	0.8
Water availability (%)	A_1	1.9	1.0	2.0	0.8	1.8	0.7	1.9	0.9
	B_2h	5.1	1.2	4.8	1.9	4.2	1.2	4.8	1.4
Water table depth (cm)									
winter		40.0	1.5	39.0	2.2	36.0	2.3	39.0	2.7
spring		55.0	4.0	59.0	5.0	60.0	6.6	56.0	5.0
summer		88.0	8.5	100.0	14.0	84.0	5.5	89.0	10.1
fall		64.0	5.0	67.0	5.1	60.0	4.6	63.0	5.3
July/77 (†)		160.0	25.6	163.0	28.1	137.0	19.0	153.0	26.0

(†) This measurement was performed during the long dry period that occurred in the area in 1977.

Table A2. Elemental concentrations in the foliage of 4-year-old *E. grandis* growing on Immokalee, Myakka, and Smyrna soils.

Soil		N	P	K	Ca	Mg	Na	Al	Mn	Cu
		Elements								
Immokalee		%						ppm		
(n=32)	Mean	1.25	0.26	0.55	1.04	0.33	0.16	72	54	5
	S.E.	0.10	0.08	0.06	0.14	0.02	0.03	25	16	1
Myakka (n=7)	Mean	1.29	0.24	0.54	0.99	0.32	0.19	79	46	4
	S.E.	0.11	0.10	0.09	0.14	0.01	0.03	27	14	2
Smyrna										
(n=11)	Mean	1.30	0.24	0.51	1.05	0.32	0.17	78	48	4
	S.E.	0.26	0.06	0.05	0.13	0.03	0.04	26	15	1
Study area										
(n=50)	Mean	1.26	0.25	0.54	1.04	0.32	0.17	74	52	4
	S.E.	0.15	0.08	0.06	0.14	0.02	0.03	25	15	1

Table A3. Growth parameters of a 4-year-old *E. grandis* plantation on Immokalee, Myakka, and Smyrna soils.

Soil		Growth parameters: Dominant height	Mean height	Mean diameter	Total volume
		-------- m --------		cm	m^3/ha
Immokalee (n=32)	Mean	12.9	10.6	9.2	35.88
	S.E.	1.6	1.6	1.4	13.39
Myakka (n=7)	Mean	13.2	10.5	9.4	36.71
	S.E.	1.2	1.3	1.3	9.75
Smyrna (n=11)	Mean	11.8	9.2	8.2	22.39
	S.E.	1.6	1.6	1.1	8.69
Study area (n=50)	Mean	12.7	10.3	9.0	33.03
	S.E.	1.6	1.6	1.4	13.16

Table A4. Simple and multiple regression equations relating tree growth to soil properties.

Soil Series	Equations	F	R^2	SEE(†)
IMS(††)	$HO = 16.34 - 2.14\ SPH + 0.21\ SAL + 0.39\ D/BTH + 10^{-4}\ OBKAL + 0.04\ BNA + 0.01\ A_1N/A_1P - 0.36\ SAK$	15.7	0.73	0.86
(n=49)	$HM = 14.25 + 0.29\ SAL - 3.24\ BPH + 0.53\ CLB + 0.42\ O/BTH + 10^{-3}\ A_1N - 0.41\ A_1OC^2$	16.8	0.70	0.92
I	$HO = 13.21 - 0.05\ BTH + 0.78\ VFSNB - 0.36\ BWA$	10.4	0.53	1.16
(n=32)	$HM = 5.84 + 0.47\ O/BTH + 0.39\ SAL$	16.9	0.54	1.11
	$VOL = 41.19 + 2.62\ SAL + 42.67\ A_2P + 17.48\ SOC - 0.61\ AKAL - 0.14\ CAKG - 31.34 \log BTH$	10.6	0.72	7.90
M	$HD = -9.02 - 0.04\ STR + 0.38\ MSNB$	131.0	0.98	0.58
(n=7)	$HM = 10.54 - 0.98\ CSNB + 0.76\ CLB$	20.4	0.91	0.46
	$VOL = -33.74 + 1.99\ A_1TH + 5.56\ SICLA$	50.4	0.96	2.30
S	$HD = 0.72 + 3.34\ SPH - 0.08\ PKG$	56.0	0.94	0.37
(n=10)	$HM = 7.15 + 0.65\ D/BTH + 22.87\ VCSNB$	17.2	0.83	0.52
	$VOL = -66.20 + 28.85\ PKCLA + 252.18\ VCSNB$	21.2	0.89	3.00
MS	$HM = 20.03 - 2.50\ BPH$	27.4	0.65	0.77
(n=17)	$VOL = 0.98 + 5.28\ SIA + 0.01\ D^2$	15.3	0.68	6.40

(†) SEE is expressed in m for HD and HM and in m^3/ha for VOL.
(††) IMS=All soil series combined; I=Immokalee; M=Myakka; S=Smyrna; MS=Myakka and Smyrna combined.

Table A5. Chemical properties of the B_2h horizon soil at the end of the experiment as influenced by Al application.

Applied Al	Soil pH 1:2 H_2O		Soil pH 1:1 N KCl		Double acid extractable P		K		Ca		Mg		Al		N KCl extractable Al	
	A_1	B_2h	A_1	B_2h	A_1	B_2h	A_1	B_2h	A_1	B_2h	A_1	B_2h	A_1	B_2h	A_1	B_2h
- ppm -					ppm											
0	3.7	3.2	2.9	2.8	2.3	103	4.0	4.0	108	127	8.0	6.7	21	370	12	160
1	3.6	3.3	2.8	2.8	4.1	94	4.0	4.0	108	119	6.7	5.3	33	376	15	140
5	3.6	3.3	2.9	2.9	4.7	105	4.0	4.0	121	135	8.0	5.3	27	386	14	132
25	3.7	3.3	2.9	2.9	4.5	85	4.0	4.0	117	116	8.0	6.7	24	376	14	165
125	3.6	3.4	2.9	3.0	6.7	92	4.0	4.0	83	100	5.3	4.0	44	420	21	143
625	3.2	3.4	3.0	3.3	12.0	93	4.0	4.0	68	72	8.0	8.0	44	526(†)	28	150(†)

(†) The Al values indicated for the application of 625 ppm Al were obtained from plots which were flushed. For the unflushed pots, in which plants had died, the values of double-acid extractable and N KCl extractable Al in the B_2h soil were 714 and 300 ppm, respectively.

Table A6. Height and fresh weight (FW) of the above-ground tree and weight and percent distribution of dry roots according to soil horizons and root class.

Plot No.	HT	FW	Horizon	Root classes: Fine		Root classes: Large		Total	
	m	kg		kg	%	kg	%	kg	%
1	13.6	71	A_1	9.5	45.3	11.4	54.7	20.9	(84.9)(†)
			A_2	1.4	39.0	2.3	61.0	3.7	(15.1)
	Sum			10.9	(44.3)	13.7	(55.7)	24.6	--
2	10.5	37	A_1	1.8	21.5	6.7	78.5	8.5	(86.7)
			A_2	0.5	37.2	0.8	62.8	1.3	(13.3)
	Sum			2.3	(23.5)	7.5	(76.5)	9.8	--
3	13.9	79	A_1	4.0	18.2	17.8	81.8	21.8	(90.4)
			A_2	1.2	52.6	1.1	47.4	2.3	(9.6)
	Sum			5.2	(21.6)	18.9	(78.4)	24.1	--
4	13.5	115	A_1	2.7	8.7	28.1	91.3	30.8	(88.2)
			A_2	1.6	38.3	2.5	61.7	4.1	(11.8)
	Sum			4.3	(12.3)	30.6	(87.7)	34.9	--
5	12.2	59	A_1	4.3	33.7	8.4	66.3	12.7	(74.3)
			A_2	1.4	30.7	3.0	69.3	4.4	(25.7)
	Sum			5.7	(33.3)	11.4	(66.7)	17.1	--
6	13.7	68	A_1	3.5	15.9	18.5	84.1	22.0	(90.1)
			A_2	0.6	25.5	1.8	74.5	2.4	(9.9)
	Sum			4.1	(16.8)	20.3	(83.2)	24.4)	---
	Total			32.5	(24.1)	102.4	(75.9)	134.9	

(†) Numbers in parentheses represent percent over the total root weight in each plot.

Table A7. Characteristics of the spodic horizons in the plots where tree root systems were excavated.

No.	Depth	Thickness	Bulk density	Soil pH 1:2 H_2O	Soil pH 1:1 N KCl	Double acid extractable P	K	Ca	Mg	Na	Al	N KCl extractable Al
	----- cm -----		g/cm^3			----------			ppm			----------
1	52	22	1.80	4.3	3.1	2	4	5	20	48	760	280
2	130	45	--	4.0	3.0	5	4	13	12	48	760	255
3	80	18	1.51	3.8	2.8	29	8	69	24	92	620	270
4	102	52	1.77	---	---	--	-	--	--	--	---	---
5	31	15	1.57	5.0	4.1	7	4	1	4	40	1160	40
6	85	22	1.69	4.2	3.0	22	8	1	16	48	1200	350

COMPUTER PROGRAM FOR RIDGE REGRESSION

```
DATA TEST;
INPUT
INT = 1;
CARDS;
;
MACRO XMATRIX TEST (KEEP=INT X1 X2 X3) %
MACRO RESPONSE TEST (KEEP=Y)%
MACRO KVALUES .05*(0:20)%
MACRO RIDGREGR
PROC MATRIX;
FETCH X DATA=XMATRIX;
FETCH Y DATA=RESPONSE;
K=KVALUES;
NK=NCOL(K);
NX=NROW(X);
NB=NCOL(X);
SYM=0: (NB-1);
DO IK=1 TO NK;
   BETA=(INV(X`*X+K(1, IK)#I(NB)))*X *Y;
   LST=LST//(K(1,IK)#J(NB,1,1)::BETA::(SYM`));
END;
OUTPUT LST DATA=RIDGEST(DROP=ROW RENAME=(COL1=K
                COL2=BETAHAT COL3=SUB));
PROC PLOT NOLEGEND;
PLOT BETAHAT*K=SUB;
TITLE RIDGE REGRESSION PARAMETER ESTIMATES;
TITLE4 VALUE PLOTTED IS PARAMETER SUBSCRIPT;
*
*  END RIDGREGR MACRO
*;%
RIDGREGR
```

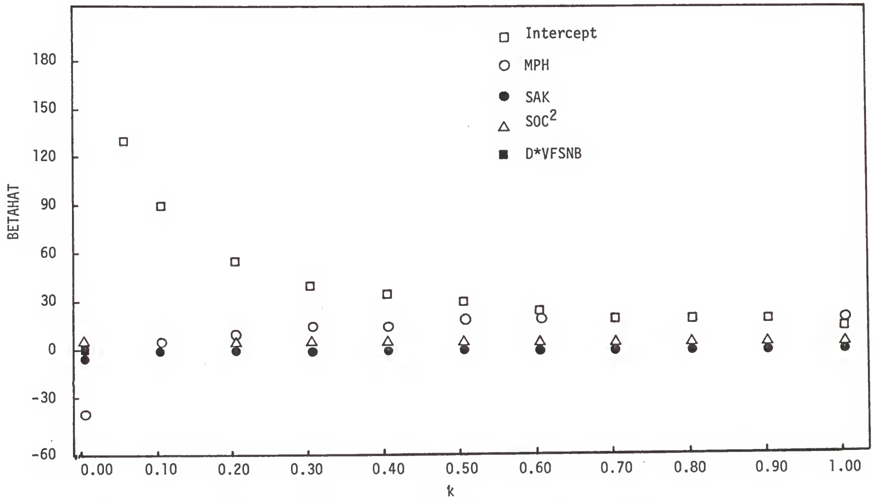

Figure A1. Variations of BETAHAT as a function of k (standardized data).

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BIOGRAPHICAL SKETCH

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Nairam Barros is married to Maura de Oliveira Barros and they have two children, Andrea, age 8, and Nairam Filho, age 4.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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